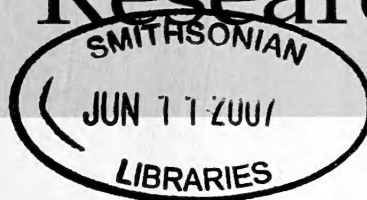




# Journal of Hymenoptera Research



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## Neotype Designation for *Anagrus atomus* (Linnaeus) (Hymenoptera: Mymaridae)

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**Abstract.**—A neotype is designated for *Anagrus atomus* (Linnaeus), the type species of the common and widespread fairyfly genus *Anagrus* Haliday (Hymenoptera: Mymaridae). An illustrated description of the neotype specimen, collected at the type locality in Uppsala, Sweden, is provided. The taxonomic status of *A. atomus* is discussed, with particular reference to the closely related species *A. ustulatus* Haliday.

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*Anagrus atomus* (Linnaeus) (Hymenoptera: Mymaridae) is an economically important egg parasitoid of various crop-damaging leafhoppers (Hemiptera: Cicadellidae) in the genera *Arboridia* Zachvatkin, *Edwardsiana* Zachvatkin, *Empoasca* Walsh, *Erythroneura* Fitch, *Neoaliturus* Distant, *Zygina* Fieber, and *Zyginidia* Haupt (Vidano and Arzone 1988, Triapitsyn 1998). *Anagrus atomus* has been recorded from numerous leafhopper species, sometimes due to misidentifications of both the host and parasitoid. It is a widely distributed species, present throughout Europe and also in Asia (China, Iran, Israel, Kyrgyzstan, Pakistan, Republic of Korea, Eastern Russia, Turkey, Turkmenistan), America (Argentina, Canada, Chile, USA), Africa (Cape Verde Islands, Egypt), and Australasia (New Zealand) (Triapitsyn and Berezovskiy 2004). Probably it was unintentionally introduced into countries such as Argentina, Chile, and New Zealand.

Linnaeus described *Ichneumon atomus* in 1767. His very brief description (p. 941), in which he specified that the habitat is Uppsala, translated from Latin, is: “it is variegated pale and fuscous, it is smaller than *Acarus sirene*, so small that it is visible

only when moving and it can be numbered among the smallest winged insects”. This description of course could fit any small, pale microhymenopteran in several families. Therefore, a study of its type is needed but unfortunately, as Fitton (1978) and Graham (1982) stated, it is not present in the collection of Linnaeus owned by the Linnean Society of London, England.

When Haliday (1833) defined the genus *Anagrus* he included two new species (*A. ustulatus* and *A. incarnatus*) and designated *Ichneumon atomus* as the type species of *Anagrus* but did not specify whether he had studied its type or not. His redescription of *A. atomus* is as brief as that of Linnaeus. Besides measurements of the body and the wings, he only stated that the head, the apex of the antennae, the prothorax and the “anus” are fuscous while the wings are hyaline and have a beautiful fringe.

Bakkendorf (1926) synonymized almost all the previously described species of *Anagrus* under *A. incarnatus*. Debauche (1948), in contrast, re-established *A. atomus* as a valid species and redescribed it. He also synonymized *A. ustulatus* under *A. atomus*, unfortunately without mentioning

whether or not he had examined Haliday's or Linnaeus' types (we suppose that he hadn't).

Chiappini (1987) redescribed *A. atomus* based on specimens from the Debauche collection and also on other specimens she captured in traps and reared from grape leaves in Italy, all of which were identified as *A. atomus* in accordance with the earlier concepts of this species (Debauche 1948, Viggiani 1970, Graham 1982). She did not designate a neotype, as, at that time, the case could not be included in the "circumstances admitted" specified in article 75 of the International Code of Zoological Nomenclature (1985). Besides, her 1987 publication was not a "revisory work", and the type of *A. atomus* could still be in Uppsala (Graham 1982). In the same paper (Chiappini 1987), based on ecological as well as morphological features, she recognized another distinct, then unnamed species which subsequently (Chiappini 1989) proved to correspond to *A. ustulatus*. By then Graham (1982) had already reinstated *A. ustulatus* as a valid taxon, designated a lectotype for it, and stated that it differed from *A. atomus* by its darker coloration, wider fore wings and, in females, by different proportions of the funicle articles.

Lately, some doubts have been raised whether *A. ustulatus*, the most closely related species to *A. atomus*, is really a different species because definitions of both taxa seemed uncertain, largely due to unavailability of the type material of *A. atomus*. In addition, other circumstances have changed since Chiappini (1987) published the first paper on the subject. First, a lot of revisory papers on *Anagrus* were published by Chiappini (1989), Chiappini et al. (1996), Chiappini and Lin (1998), Triapitsyn (1997, 1998, 1999, 2001), and Triapitsyn and Beardsley (2000). Second, Mats Eriksson (curator of the Zoology Section) and Hans Mejlön (curator of the entomological collections) thoroughly searched the Linnaeus collection at the Museum of Evolution (Uppsala Universi-

ty), but were "unable to find anything like Mymaridae in their holdings" (M. Eriksson, pers. comm.). Third, specimens according to Haliday's (1833) brief redescription as well as to Debauche's (1948) and Graham's (1982) concept of *A. atomus* were captured in Uppsala, Sweden, the type locality of *Ichneumon atomus*, by Fredrik Ronquist, formerly of the Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University. Several other *Anagrus* species were also captured at the type locality (Triapitsyn and Berezovskiy 2004) but, of these, the only species belonging to the *atomus* species group (Chiappini 1989) was *Anagrus ustulatus* (see Comments for the diagnosis).

Therefore, considering that the identity of *A. atomus* has long been in doubt, that no specimen(s) of *Ichneumon atomus* are present in either the Linnaeus collections at Uppsala or London, that no neotype has ever been designated for the type species of *Anagrus*, that all described species of this genus (for which type specimens exist) have been carefully revised by us, and that fresh material from the original type locality is available, it now seems appropriate to designate here a neotype for *A. atomus* (Linnaeus). Its description follows; an abbreviation used in the text is: F = an antennal funicle article.

### *Anagrus (Anagrus) atomus* (Linnaeus)

(Figs 1–3)

*Ichneumon atomus* Linnaeus, 1767: 941.

*Anagrus atomus* (Linnaeus): Haliday, 1833: 347; Chiappini, 1989: 102–104 (diagnosis, synonyms, and list of earlier citations); Triapitsyn and Berezovskiy, 2004 (distribution).

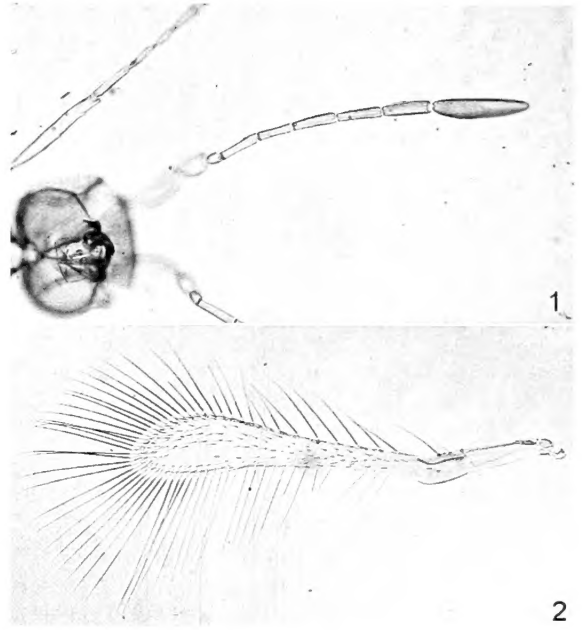
*Type material*.—Neotype female of *Ichneumon atomus* Linnaeus, 1767, here designated in accordance with ICZN Article 75 (ICZN 1999), on slide, labelled: 1. "*Ichneumon atomus* Linnaeus, 1767 = *Anagrus atomus* (Linnaeus 1767) (Hymenoptera: Mymaridae) NEOTYPE [female symbol] Des. by S. Triapitsyn & E. Chiappini



2003"; 2. "SWEDEN: Uppsala, Hågadalen, 26.viii-5.ix.1990, F. Ronquist, MT baited with rotten meat. Mounted at UCR/ERM by V. V. Berezovski 2002 in Canada balsam". The neotype was borrowed from the Canadian National Collection of Insects, Ottawa (CNCI). By agreement with John Huber at the CNCI the neotype will be deposited in the Museum of Evolution, Uppsala University, Uppsala (UZI). The neotype is in good condition, mounted in Canada balsam under two coverslips, one containing the wings (detached from the body), and the other the rest of the body (cleared in KOH prior to slide mounting).

**Other material studied.**—Three other specimens of *A. atomus* were collected at or near the same locality as the neotype. Their collection data and depositories are as follows: 1 female on slide [CNCI]: SWEDEN: Uppland Uppsala, Hågadalen, 17–26.viii.1990, F. Ronquist, MT. 1 female on card [CNCI]: SWEDEN: Uppsala, Hågadalen, 26.viii-5.ix.1990, F. Ronquist, MT baited with rotten meat (same data as the neotype). 1 female on card [Entomology Research Museum, University of California, Riverside, California, USA (UCRC)]: SWEDEN: Uppland Uppsala, Eriksberg, 30.vii-11.viii.1986, F. Ronquist, MT/PT. Two females and a male in the Oxford, England, part of the Haliday collection, labelled respectively as W21 "*Anagrus atomus* Linn Haliday Coll.", W20, and W16 were also examined.

**Description.**—**Color:** Head brown, except vertex mostly light brown (stematicum brown), eyes and ocelli red; scape and pedicel light brown, flagellum brown (apical flagellomeres slightly darker); pronotum, posterior half of mesoscutum, anterior scutellum, metanotum and propodeum light brown, anterior half of mesoscutum and axillae brown, posterior scutellum pale; wing venation brown; legs light brown (tarsi a little darker); gastral terga brown, with light brown membranous bands between them.



Figs 1–2. *Anagrus atomus* (Linnaeus), neotype female. 1. Antenna. 2. Fore wing.

**Head:** About as wide as mesosoma. Antenna (Fig. 1) sparsely setose; scape 3.6 x as long as wide and 2.2 x as long as pedicel; F1 oval, much shorter than pedicel and shortest of funicle articles; F2 a little longer than F3 and slightly shorter than F4 or F5 which are equal in length, F6 longest and broadest of funicle articles; longitudinal sensilla on F4 (1), F5 (1) and F6 (2); clava a little longer than two preceding articles combined, with three longitudinal sensilla positioned subapically.

**Mesosoma:** A little shorter than metasoma. Mesoscutum finely longitudinally striate, without adnotaular setae. Fore wing (Fig. 2) 6.8 x as long as wide; distal macrochaeta about 2.5 x length of proximal macrochaeta; fore wing blade slightly infuscated behind venation but otherwise hyaline, with distinct bare area in broadest part next to posterior margin, discal microtrichia arranged in 3 or 4 irregular rows; longest marginal cilia 2.9 x maximum fore wing width. Hind wing hyaline; disc with a few microtrichia at apex and a row of microtrichia along posterior margin.

**Metasoma:** Ovipositor almost reaching mesophragma anteriorly and a little ex-

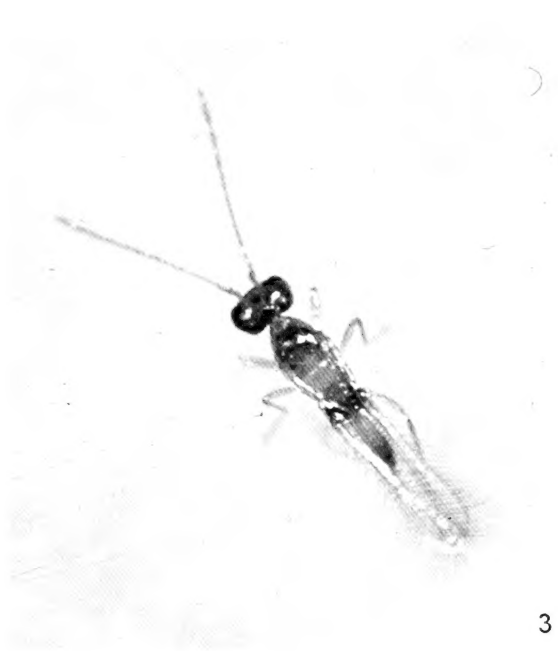


Fig. 3. *Anagrus atomus* (Linnaeus), female (from egg of a grape leafhopper, Verago, Piacenza, Italy).

serted beyond apex of gaster posteriorly (by about 1/15 of its total length). External plates of ovipositor with one seta each. Ovipositor length/ foretibia length 1.9:1.

Measurements (in micrometers,  $\mu\text{m}$ ).—Body length (taken before slide mounting) 559; head length/width (length taken before slide mounting) 100:161; mesosoma 209; metasoma 281; ovipositor 236. Antenna: scape 75; pedicel 34; F1 17; F2 44; F3 39; F4 48; F5 48; F6 52; clava 107. Fore wing length/width 546:80; longest marginal cilia 233. Hind wing length/width 500:23; longest marginal cilia 179. Legs (given as coxa, trochanter, femur, tibia, tarsus): fore 66, 42, 130, 124, 155; middle 48, 39, 124, 173, 158; hind 70, 40, 120, 188, 164.

*Diagnosis.*—*Anagrus atomus* can be distinguished from all other species of the *atomus* species group, as defined by Chiappini et al. (1996), by the following combination of features: F3 without longitudinal sensilla, F4 longer than the previous articles and bearing one longitudinal sensillum, F2 and F3 together much longer than F6, at least by half their combined length, mesoscutum without adnotaular

setae, hairless area present only at broadest part of fore wing, and fore wing length/width less than 10.

*Comments.*—Specimens of *A. atomus* from vineyards in southern Europe (e.g., Italy and France) may show a different color pattern on the gaster, with the terga from about fourth to seventh yellow (Fig. 3), whereas the northern forms appear to be slightly darker or more uniformly colored.

The three specimens labeled as W21, W20, and W16 in the Oxford part of the Haliday collection clearly belong to *A. atomus*, as correctly stated by Graham (1982).

We also re-examined the lectotype male of *A. ustulatus* Haliday ( $n^\circ$  70), together with the two female specimens ( $n^\circ$  72 and 73) under this name in the Haliday collection at the National Museum of Ireland, in Dublin, in order to verify the possible synonymy of *A. ustulatus* under *A. atomus*. The lectotype agrees with what had already been stated by Graham (1982) and Chiappini (1989); namely, the ratio between the lengths of the macrochaetae on the fore wing marginal vein is greater than two, the fore wing has a hairless area on the disc, and it is very wide compared to that of *A. atomus*. The male genitalia, which had already been studied by Chiappini (1989) who stated (contrary to Graham) that they were typical of the *atomus* species group, were not checked again because to do so would require ungluing the type specimen. In contrast to the lectotype of *A. ustulatus* the ratio between the lengths of the macrochaetae is less than two in the females  $n^\circ$  72 and 73, as is typical of members of the *incarnatus* species group of *Anagrus*. Therefore, these two females cannot be conspecific with the lectotype of *A. ustulatus* as they belong to a different species group. In addition, the fore wings of females  $n^\circ$  72 and 73 are narrower and without a bare area on the disc and F2 is the longest, unlike either *A. atomus* or *A.*

*ustulatus*. Specimens n° 72 and 73 belong to *A. incarnatus*, according to the most recent concept of this species (Triapitsyn 1997).

Therefore, the species concept for *A. ustulatus* should be based only on the lectotype designated by Graham (1982). This male has fore wing proportions different from *A. atomus* males but equal to those of the males of the *Anagrus* species found on bramble and rose (Chiappini 1987) and whose females differ from those of *A. atomus* by F4 being as long as F3 and without longitudinal sensilla (Chiappini 1989), and by the fore wing being wider. Many other data, both ecological (Chiappini 1987) and chemical, support the separation of *A. atomus* from *A. ustulatus*. For example, the cuticular hydrocarbon patterns in these two species differ considerably, as the second species displays a notable amounts of alkenes not present in the first's pattern (Floreani et al. in prep.). On the basis of this knowledge, we treat *A. ustulatus* as specifically distinct from *A. atomus*, even though we know that more studies, particularly of field populations of *Anagrus*, are needed to better characterize these two species.

## ACKNOWLEDGMENTS

We thank John T. Huber (CNCI) for the loan of material and review of an earlier draft of the manuscript, and Mats Eriksson and Hans Mejlön (UZI) for searching for the type of *A. atomus* and Mymaridae in general in the Linnean collection in Uppsala. Vladimir V. Berezovskiy (UCRC) helped with specimen preparation.

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## The Effect of Gland Secretions on Escape Chewing in *Melittobia* (Hymenoptera: Eulophidae), Including Cross-species Investigations

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**Abstract.**—*Melittobia* is a genus of small, gregarious idiobiont parasitoids in the family Eulophidae. Following emergence as adults, females form circles in which they cooperate to chew an escape hole from the host cells in which they developed. Dry milked crude venom, which could contain constituents from the alkaline gland as well as the venom reservoir, has been shown to elicit chewing in *M. digitata*. Here we investigated whether a related species (*M. femorata*) chewed in response to compounds in its dissected venom reservoir plus alkaline-gland, and whether crude venom milked from a member of another species group (*M. australica*) would also elicit chewing in *M. digitata*. *Melittobia femorata* chewed significantly more at combined gland and reservoir extract-marked spots than at controls. To examine the crude venom's effect across species we marked spots with milked *M. australica* venom, and introduced female *M. digitata* wasps. These milked crude venom spots elicited chewing similar to that elicited by that of *M. digitata* marked spots, and the response to either's venom was significantly different from blank controls. Possible reasons for the lack of a high level of specificity in the chewing response to a pheromone are discussed.

---

*Melittobia* Westwood is a cosmopolitan genus of small gregarious parasitic wasps (Balfour-Browne 1922, Buckell 1928, Dahms 1984b). They are commonly found attacking mud dauber (Hymenoptera: Sphecidae) prepupae and their associates (Matthews 1997), but also attack a wide range of solitary bees and wasps and their associates (Balfour-Browne 1922, Krombein 1967).

When attacking a mud dauber wasp they have to escape from the thick-walled mud nest, yet females do not have noticeably well developed mandibles. Donovan (1976) observed *M. hawaiiensis* Perkins females circled around another female that had started chewing a pit in the mud wall, and speculated that they then cooperated in chewing their way out. Subsequently, such cooperative chewing has been observed in several *Melittobia* species (L.D. Deyrup unpublished).

Deyrup et al. (2005) reported that chewed pits invariably had associated sting marks and showed that a putative pheromone in the milked crude venom, which most likely contains constituents of the alkaline gland as well as the venom reservoir, of *M. digitata* Dahms elicited chewing from conspecific females. Because similar chew pits made by other species of *Melittobia* also typically show sting marks in their centers (Deyrup unpublished), we decided to investigate whether extracted venom components would elicit chewing in a closely related species, *M. femorata* Dahms (Dahms 1984a).

Such chewing, if demonstrated, could be in response to a normal constituent of crude venom, or blend of odors. Regardless, it is difficult to envision selection pressure sufficient to cause evolutionary divergence in such a cue, since there appear to be no negative effects of co-



operative escape chewing, even among unrelated females.

## METHODS

In general the methods follow those described by Deyrup et al. (2005). *Melittobia australica* Girault responded to the venom-milking procedures described in Deyrup and Matthews (2003), yielding adequate amounts of crude venom for the experiment. However, *M. femorata* does not respond to this venom-milking technique. Therefore, as an alternative we dissected the lower reproductive tract of females in insect saline [10 mM sodium phosphate, 0.9% (w/v) NaCl, pH 8.0]. While there are many possible pheromone sources in the female reproductive system, the two most likely are the alkaline gland and venom reservoir. These were separated from the ovipositor and combined for use in the experiment. Since milked crude venom used in previous work could contain a combination of the fluids contained in both organs we decided to combine them for this experiment.

As described in Deyrup et al. (2005), 20 plastic box lids were prepared for the first set of experimental treatments by making four pin indentations, one in each corner of the inner side. We then smeared the combined alkaline gland and venom reservoir dissected from a single female of *M. femorata* into one pin indentation and repeated this using a fresh female applied to the pit on the opposite corner. The other two pits served as controls for chewing stimulated by the pit alone as in Deyrup et al. (2005). Treated lids were then placed on 20 boxes of 250–300 1–3 day old mated *M. femorata* females and left for 12 hours in complete darkness at 25°C, after which they were examined for evidence of chewing at each of the four pits.

To determine if *M. australica* or *M. digitata* would be stimulated to chew by *M. australica* crude venom, we set up a two more series of boxes. Three corner circles were drawn on the lids as in Deyrup et al.

(2005) and randomly assigned one of three treatments. One circle received 1 FED (female equivalent dose) of milked *M. australica* venom. In another circle a clean pin rub served as a negative control, and the third circle was 1 FED of milked venom from a *M. digitata*. Fifteen of these lids were prepared for each series, and placed on boxes of 250–300 females as before. Boxes were then placed in absolute darkness at 25°C, and scored for signs of chewing 12 hours later.

Cochran Q tests were used to analyze chewing frequencies (Statistica 6.0). This test was chosen because the treatments were paired, and the results were scored as chewing presence or absence (1 or 0 respectively).

## RESULTS

The experimental group containing smeared *M. femorata* venom reservoir and alkaline gland contents elicited chewing from *M. femorata* in at least one of the two treated pits in 19 of the 20 replicates. In contrast, both control pits were chewed on only two occasions out of 20. These differences were highly significant ( $P < 0.0001$ ,  $Q = 17.0000$ , 1 df). In the series to determine if *M. australica* chewed at their own milked crude venom or the milked crude venom from *M. digitata*, there was no chewing what-so-ever at any treatment or control.

In the experiment to examine if chewing was elicited in *M. digitata* by milked crude venom from *M. australica*, chewing occurred in 9 of the 15 replicates (Table 1). The overall Cochran test was significant ( $P < 0.0031$ ,  $Q = 11.5556$ , 2 df). Therefore, using Fisher's test for multiple analyses, we ran pairwise Cochran tests that revealed a significant difference between the blank and *M. australica* venom ( $P < 0.0047$ ,  $Q = 8.0$ , 1 df), and the blank and *M. digitata* venom ( $P < 0.0143$ ,  $Q = 6.0$ , 1 df). There was no significant difference between chewing at the positive control, *M. digitata* venom,

Table 1. Chewing response by *M. digitata* females after 12 hours exposure of treatment circles containing venom milked from either *M. digitata* or *M. australica*. Different letters in the "Significance" column indicate significant differences using a Cochran Q test  $p < 0.05$ ,  $df = 1$  (Statistica 6.0).

Treatment	Chewed	Replicates	Significance
<i>M. australica</i> venom	9	15	a
<i>M. digitata</i> venom	7	15	a
Control	1	15	b

and *M. australica* venom ( $P < 0.3173$ ,  $Q = 1.0$ , 1 df).

DISCUSSION

The *M. femorata* chewing results in response to dissected *M. femorata* reproductive tract organs suggest that *M. femorata* has a pheromone in its crude venom that stimulates chewing at a particular spot. This adds support to the idea that chewing in response to crude venom components evolved before the speciation event that separated *M. digitata* and *M. femorata*.

The negative results for *M. australica* chewing are hard to interpret since the design does not allow us to test a "lack of stimulus". The species has been observed to cooperatively chew. There could be many reasons for the crude venom not to be attractive such as the possibility that other factors are necessary or that chewing only occurs during a particular unestablished window of opportunity. More rigorous experimentation would be required to establish that the crude venom is not at least a part of the chewing stimulus.

The positive results for the attraction of *M. australica* crude venom for *M. digitata* females (Table 1) might seem surprising since the two species belong to different species groups (Dahms 1984a). Especially since we were unable to elicit chewing in response to milked crude venom for *M. australica*. However, there is little reason to expect that such a pheromone, if there is a pheromone for chewing in *M. australica*, would not be conserved, since

a mutation could leave carriers trapped in the host's cell. Even if there is no such pheromone present in crude venom for chewing in *M. australica*, the chemical that stimulates chewing for *M. digitata* could be one that is stable and under selection for another purpose (e.g., perhaps containing a constituent causing developmental delay in the host [Deyrup et al. 2003]). Components of other pheromones appear to have been conserved in *Melittobia*. Matthews et al. (1985) found that females of *M. digitata*, *M. femorata*, and *M. australica* were attracted to non-conspecific as well as conspecific males in choice tests. Further work should be done on investigating the source of the pheromone in which either the venom reservoir or the alkaline gland is presented alone and together.

ACKNOWLEDGEMENTS

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**Four New Species of the Wasp Genus *Celonites* Latreille, 1802  
(Hymenoptera: Vespidae: Masarinae) from South-western Africa,  
Designation of Neotype for *C. michaelsoni* von Schulthess, 1923, Species  
Representation in Namibia, and Key to Species Occurring in Namibia**

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*Abstract.*—Four new species of the genus *Celonites* Latreille, 1802 (Hymenoptera: Vespidae: Masarinae) are described from south-western Africa: *heliotropii* and *pulcher* from Namibia, *kalahariensis* from Namibia and the adjacent trans-Orange part (Gordonia) of the Northern Cape of South Africa, and *arenarius* from the north-western corner (Richtersveld) of the Northern Cape. A neotype is designated for the widespread, chiefly Namibian *Celonites michaelsoni* von Schulthess, 1923, with which *C. gariepensis* Gess, 1997 is sunk into synonymy. Namibian records are given for *C. andrei* Brauns, *C. capensis* Brauns, *C. clypeatus* Brauns, and *C. tumidiscutellatus* Gess, all better known from South Africa. Distribution maps are given for all nine species and forage plant records are included for eight. A key to the species of *Celonites* occurring in Namibia is given.

*Key words.*—Hymenoptera, Vespidae, Masarinae, *Celonites*, new species, Namibia, southern Africa

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The genus *Celonites* Latreille was revised by Richards (1962) as part of his study of the Masarinae of the world. He dealt with a total of 26 species from the Palearctic and Afrotropical regions, eight species being from southern Africa. Amongst a number of species mentioned but not examined by Richards was one additional southern African species, *C. michaelsoni* von Schulthess from the present day Namibia, known only from the holotype which he rightly believed to have been destroyed in Hamburg during World War 2.

Since 1962 seven additional species have been recognised from southern Africa, three described by Gess (1997) and four described in the present paper. The discovery of these species resulted from purposeful collecting in under-collected parts of the Western and Northern Cape, South Africa and particularly in Namibia. The overall known distribution of the genus in southern Africa has been given by Gess and Gess (2004b: Fig. 7).

As no *Celonites*, other than the single specimen of *C. michaelsoni*, have previously been recorded from Namibia, particular attention is paid to the fauna of that country from which eight species are now known: the here recognized and widespread *C. michaelsoni* von Schulthess, *C. heliotropii* sp. nov., *C. pulcher* sp. nov., *C. kalahariensis* sp. nov. and four species previously known from South Africa, *C. andrei* Brauns, *C. capensis* Brauns, *C. clypeatus* Brauns, and *C. tumidiscutellatus* Gess. It is highly probable that *C. arenarius* sp. nov., described from the southern bank of the Orange River, will also be found in Namibia.

The key is restricted to those species occurring in Namibia. A key to all the southern African species was attempted but was found to be impracticable at the present time due to the paucity of material of some species.

The notation used for expressing geographic co-ordinates is as in the gazetteer

of *The Times Atlas of the World* (1981). The figures before the stop are degrees, those after the stop are minutes; the stop is **not** a decimal point.

For purposes of plotting distributions, co-ordinates have been given in square brackets in the text for those localities for which none are given on the data labels.

On a few data labels from collections other than that of the Albany Museum the collecting locality is followed by degree latitude and degree longitude and by half- and quarter-degree reference letters (e.g., 3218BB) according to the Degree Reference System of Leistner and Morris (1976). As this system is not universally understood an attempt has been made here to find on a map the localities concerned and to add in square brackets the co-ordinates expressed in the manner adopted in this paper (e.g., 3218BB [32.11S 18.54E]).

In listing the material examined, the localities have been arranged, as far as practicable, in north to south order within Namibia or, in the case of South Africa, within provinces.

Acronyms here used for institutions in which material is housed are: AMG = Albany Museum, Grahamstown, South Africa; CAS = California Academy of Sciences, San Francisco, United States of America; NCP = National Collection of Insects, Pretoria, South Africa; NNIC = Namibian National Insect Collection, Windhoek, Namibia; ZMH = Zoologisches Museum Hamburg, Hamburg, Germany.

## DESCRIPTIONS OF SPECIES AND COLLECTION DATA

### *Celonites heliotropii* Gess, new species

*Celonites* sp. (undescribed): Gess and Gess, 2004a: 39 (flower visiting).

*Diagnosis*.—Both sexes: relatively small (5.6–7.3 mm); black, with pronotum, tegula, scutellum and terga reddish brown; clypeus and frons without carinae. Fore femur, particularly in female, postero-

ventrally produced in proximal half (Fig. 10). Male: most of mandibles, entire labrum and clypeus; variably developed facial markings and in some specimens underside of proximal flagellomeres, lemon yellow. Male genitalia as in Fig. 1.

*Description*.—**Female**: Black. The following are dark reddish-brown: distal half of mandible; underside of antennal club; pronotum; tegula; scutellum and median part of metanotum; in some specimens large spot anteriorly on mesopleuron, propodeal lamella laterally; in great majority of specimens terga I – VI (except for black bases); sterna I, II and VI and lateral and posterior margins of III – V; femur (distally), tibia and tarsi of all legs. Wings browned.

Length 5.8–7.3 mm (average of 4: 6.6 mm), length of front wing 4.4–5 mm (average of 4: 4.7 mm), hamuli 7 or 8; length of extended tongue 3.9 mm.

Head  $1.3\times$  as wide as long (measured across eyes and from vertex to bottom of emargination of clypeus respectively), frons and clypeus not carinate. Clypeal disc markedly raised, with surface finely reticulate punctate and with microsculptured interstices; frons, vertex and occiput more coarsely reticulate punctate, with smooth and shiny interstices. Frons slightly raised above and between antennal sockets and very slightly depressed medially above swollen area.

Pronotum, mesoscutum, mesopleuron, scutellum and dorso-lateral part of propodeum similarly punctured to frons and vertex, shiny. Scutellum gently convex, anteriorly not raised above level of mesoscutum. Tegula circa  $1.9\times$  as long as maximum width, posteriorly narrowed with outer margin curving inwards towards rounded but acute posterior angle.

Propodeal declivity markedly longitudinally rugoso-punctate. Lateral lamella of propodeum broad, with surface in same plane as adjacent median part, its outer margin minimally curved, its apex truncate, separated from median part by



narrow incurved slit. Terga more finely and closely punctured than thorax; interstices microsculptured; postero-lateral angles produced, acutely pointed; hind margins entire (non-crenulate).

Fore femur (Fig. 10, with for comparison the unmodified front leg of *C. michaelsoni*, Fig. 11) postero-ventrally produced in proximal half; end of tibia when folded against femur coinciding with produced region; tarsus short (only  $1.2\times$  tibial length); underside of tibia with moderately dense, short setae, tarsus setose throughout but with setae particularly dense on underside of tarsomeres I – IV where forming stiff brush.

**Male:** Black. The following are lemon yellow: most of mandible; entire labrum and clypeus; variably developed supraclypeal spot medially on frons; usually small to minute spot in lower half of ocular sinus; in some specimens underside of proximal flagellomeres. The following are various shades of reddish-brown: flagellomeres; pronotum (colour grading almost to yellow on humeral angle; tegula (colour grading almost to yellow anteriorly); scutellum and median part of metanotum; large spot anteriorly on mesopleuron; propodeal lamella laterally; transverse bands on terga I – VI (colour of each band dark adjacent to black base, lighter posteriorly, grading almost to yellow on postero-lateral angles); sterna I – VI (partially) and VII (totally); femur (distally), tibia and tarsi of all legs (streaks on tibiae almost yellow). Wings lightly browned (paler than those of female).

Length circa 5.6 mm; length of front wing circa 3.9 mm; hamuli 6; length of extended tongue circa 3 mm.

More gracile than female but structurally similar, apart from usual more markedly swollen antennal club and more pronounced postero-lateral angles of terga.

Genitalia in ventral view as in Fig. 1; in dorsal view with parameres distally subtruncate, posterior margin of each paramere gently concavely curved from round-

ed inner posterior angle to protruding but rounded outer (lateral) posterior angle.

*Etymology.*—The name *heliotropii*, genitive singular, is formed from the generic name of the plant *Heliotropium tubulosum* (Boraginaceae) to the flowers of which the wasp appears to be restricted for purposes of foraging for nectar or nectar and pollen.

**Material examined.**—Holotype: ♀, **NAMIBIA:** 19 km SSW of Uis on road to Henties Bay (21.27S 14.45E), 18.iv.2002 (F. W. and S. K. Gess) (visiting white flowers of *Heliotropium tubulosum* E. Mey. ex DC., Boraginaceae) [AMG]. Paratypes: **NAMIBIA:** near Palmwag (19.53S 13.55E), 26.iii.2004, 1 ♀ (visiting white flowers of *Heliotropium tubulosum* E. Mey. ex DC., Boraginaceae); Two Palms, near Palmwag (19.53S 13.54E), 27.iii.2004, 8 ♂♂ (visiting white flowers of *Heliotropium tubulosum*); same locality, 28.iii.2004, 13 ♀♀ (visiting white flowers of *Heliotropium tubulosum*); Uis to Omaruru (21.14S 15.00E), 14.iii.2004, 13 ♀♀ (12 ♀♀ visiting white flowers of *Heliotropium tubulosum*); 19 km SSW of Uis on road to Henties Bay (21.27S 14.45E), 17.iv.2002, 6 ♀♀, (3 ♀♀ visiting white flowers of *Heliotropium tubulosum*; 1 ♀ associated with hole in ground; 1 ♀ on ground); same locality, 18.iv.2002, 8 ♀♀, 1 ♂ (7 ♀♀, 1 ♂ visiting white flowers of *Heliotropium tubulosum*; 1 ♀ on ground); Gross Spitzkuppe (21.51S 15.12E), 19.iv.2002, 6 ♀♀ (visiting white flowers of *Heliotropium tubulosum*); 77 km E of Henties Bay on road to Klein Spitzkuppe (21.54S 14.58E), 19.iv.2002, 13 ♀♀ (visiting white flowers of *Heliotropium tubulosum*); 58 km SW of Usakos on road to Swakopmund (22.12S 15.10E), 23.iv.2002, 9 ♀♀, 1 ♂ (7 ♀♀, 1 ♂ visiting white flowers of *Heliotropium tubulosum*; 2 ♀♀ on ground next to *Heliotropium tubulosum*); 33 km by road from Swakopmund to Usakos, near Rössing Mtn. (22.34S 14.49E), 22.iv.2002, 1 ♀; same locality, 28.iv.2002, 1 ♀ (at *Heliotropium tubulosum*) – (all F. W. and S. K. Gess) – [all AMG]; Karibib District, 15 km W Karibib [21.56S 15.43E], 26.ii.1990, 1 ♂; Karibib District, 55 km SW Usakos [22.16S 15.08E], 1.iii.1990, 1 ♀; Karibib District, 65 km SW Usakos [22.20S 15.05E], 24.ii.1990, 2 ♀♀, 1 ♂ – (all W. J. Pulawski) [all CAS]; Damaraland, 6 km N Arandis (22.22S 14.59E), 3–31.vii.1984, 1 ♀, 8.v.–5.vi.1984, 2 ♀♀, 5.vi.–3.vii.1984, 2 ♀♀ (all J. Irish; H. Liessner); same locality, 9.iv. – 6.v.1985 (J. Irish, H. Rust), 1

♀; Swakopmund Dist., Rössing Mine (22.28S 15.02E), 13.iii.–10.iv.1984, 2 ♀♀, 10.iv.–8.v.1984, 1 ♀ (both J. Irish; H. Liessner); Swakopmund Dist., Upper Panner Gorge (22.29S 15.01E), 10.iv.–8.v.1984 (J. Irish; H. Liessner), 5 ♀♀; Swakopmund Dist., Upper Ostrich Gorge (22.29S 14.59E), 13.iii.–10.iv.1984, 2 ♀♀, 10.iv.–8.v.1984, 2 ♀♀ (both J. Irish; H. Liessner); same locality, 12.ii.–11.iii.1985, 1 ♀, 1 ♂, 9.iv.–6.v.1985, 1 ♀ (both J. Irish; H. Rust); Swakopmund Dist., Lower Ostrich Gorge (22.30S 14.58E) 13.iii.–10.iv.1984 (J. Irish; H. Liessner), 1 ♀; same locality, 12.ii.–11.iii.1985, 1 ♂, 9.iv.–6.v.1985, 1 ♀ (both J. Irish; H. Rust) – [all NNIC].

**Geographic distribution.**—(Fig. 12): Known only from Namibia, collection localities being north, northeast and east of Swakopmund in the Mopane Savanna, the Central Namib, and the Semi-desert and Savanna Transition of Giess (1971).

**Floral associations.**—Boraginaceae (*Heliotropium tubulosum* E. Mey. ex DC).

**Discussion.**—At four localities the species has been found foraging on the flowers of *Heliotropium tubulosum* in company with the masarine *Jugurtia namibicola* Gess which similarly appears restricted to this plant (Gess and Gess 2004: 39, Gess 2004: 709). *Celonites heliotropii* is the only southern African *Celonites* known to forage on *Heliotropium*, however, *C. jousseumei* du Buysson has been recorded on flowers of this genus in the Sudan and in Cyprus. G. A. Mavromoustakis found *C. cyprius* de Saussure and *C. rugiceps* Bischoff to be confined to *H. ?villosum* Willd. and to *H. europaeum* L. respectively (Richards 1962: 224).

### *Celonites pulcher* Gess, new species

*Celonites* sp. nov. F: Gess and Gess, 2003: 41 (flower visiting).

**Diagnosis.**—Both sexes: (7.2–7.9 mm); black or in some specimens with ground colour of pronotum, mesopleuron, scutellum, propodeum and gaster largely reddish brown; head, pronotum, mesopleuron, tegula, propodeum and gaster with yellowish-white markings. Clypeus

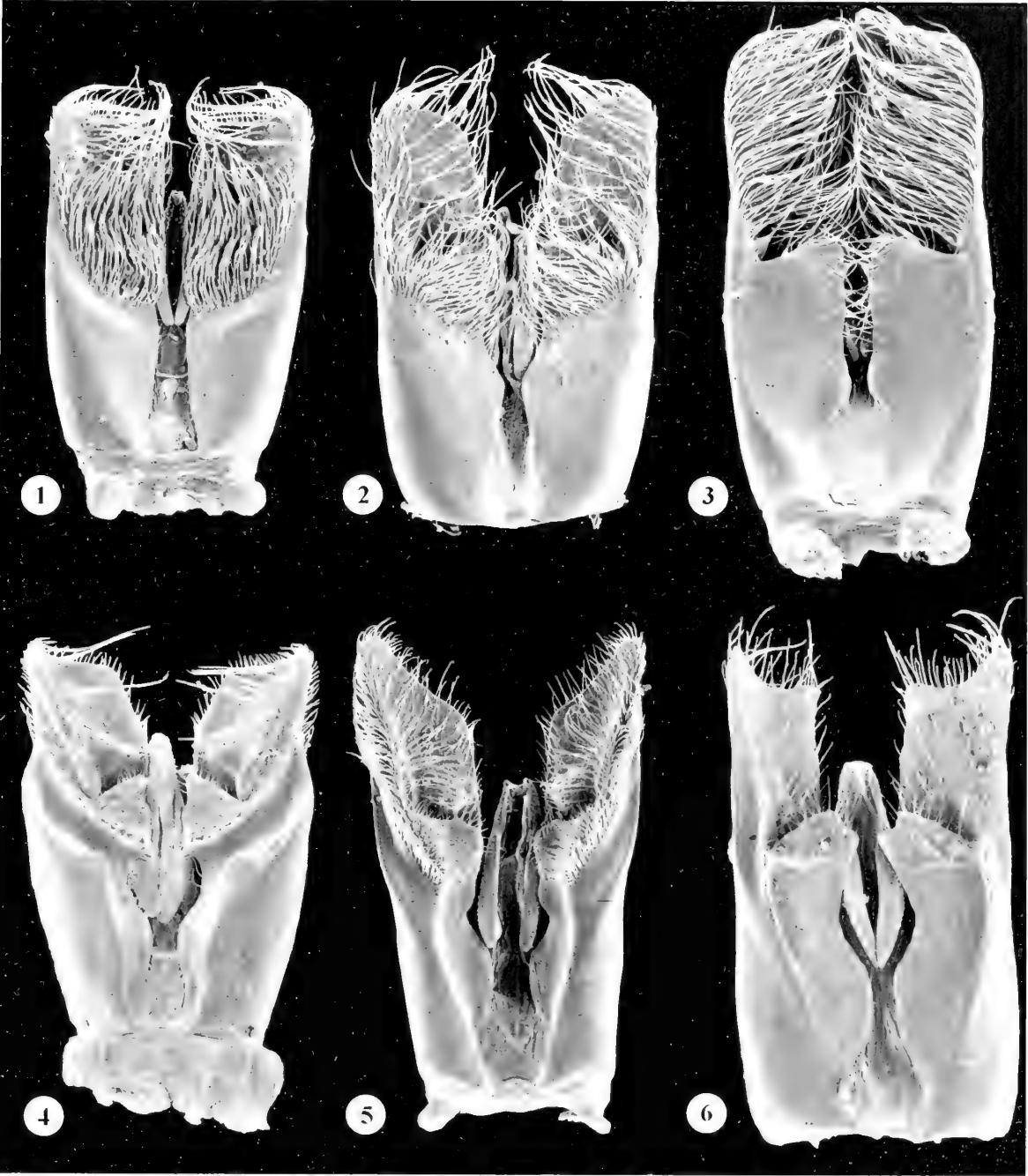
and frons carinate, shiny, with small, well separated punctures and smooth interstices. Propodeum laterally with long, anteriorly directed, narrow, sinuous slit; median part of propodeum postero-laterally markedly produced into lamella. Male genitalia as in Fig. 2.

**Description.**—**Female:** Black. The following are yellowish-white: spot on upper half of clypeus between converging arms of M-shaped carina; streak margining inner orbit from immediately above end of frontal carina to level of lateral ocellus; spot on humeral angle and narrow band (widened medially) along hind margin of pronotum; elongate spot anteriorly on mesopleuron; tegula anteriorly and posteriorly; in some specimens small spot medially on scutellum and narrow streak on metanotum laterally; posterior two-thirds of lateral propodeal lamella; lateral and medial transverse markings posteriorly on terga I – V; medial round spot on tergum VI.

Specimens from the north of the species' range differ markedly from those from the south in having the black largely replaced by reddish brown, all specimens, however, having the mandible and antenna light reddish-brown.

In the southern, melanistic specimens the following are dark reddish brown: ill-defined area anterior to yellowish-white posterior band on pronotum, tegula medially; extreme apex of scutellum, metanotum medially; diffuse patches between pale markings posteriorly on terga I and II; tibiae and tarsi.

In northern specimens the following are light reddish-brown: labrum; in some specimens diffuse area on clypeus surrounding pale spot, diffuse area on frons medially between arms of V-shaped carina and diffuse area on vertex behind eye; pronotum (other than for pale markings); in some specimens an ill-defined, posteriorly directed, V-shaped marking medially and a lateral marking posteriorly on mesonotum; upper half of mesopleuron



Figs 1–6. *Colonites* species. Ventral view of male genitalia ( $\times 50$ ). 1, *C. heliotropii*. 2, *C. pulcher*. 3, *C. michaelsoni*. 4, *C. kalahariensis*. 5, *C. tumidiscutellatus*. 6, *C. arenarius*.

(other than for pale anterior spot); tegula medially; entire scutellum and metanotum (other than for pale markings sometimes present); median part of propodeum entirely or partially (sometimes only posterior lamella); metasoma (other than for pale markings listed above), black de-

clivity of tergum I and narrow black anterior transverse bands (usually hidden) on terga II - VI; femora, tibiae and tarsi of all legs.

Wings browned in all specimens.

Length 7.2–7.9 mm (average of 6: 7.5 mm); length of front wing 5.3–6.0 mm

(average of 6: 5.5 mm); hamuli 7–9. Length of extended tongue 5.6–5.8 mm; tongue length:body length = 0.74.

Head  $1.4\times$  as wide as long (measured across eyes and from vertex to bottom of emargination of clypeus respectively). Clypeus and frons shiny, with small well separated punctures and smooth interstices; vertex dull, rugoso-punctate. Clypeus at mid-height with well-defined, smooth, widely and shallowly M-shaped carina and below it on each side with subtransverse, unpunctured, subcarinate swelling; surface of clypeal disc above M-shaped carina raised, especially laterally, below M-shaped carina (that is between it and subcarinate swelling) concave. Frons with conspicuous, smooth, widely and shallowly V-shaped carina (its arms somewhat sinuous) arising on each side opposite but outside middle of ocular sinus and meeting medially at obtuse angle at level of upper margin of antennal sockets; surface of frons falling very steeply from carina to antennal sockets and medially overhanging clypeal base.

Pronotum, mesopleuron, mesoscutum, scutellum and mesodorsal part of propodeum more coarsely sculptured than head, markedly longitudinally reticulate-punctate. Scutellum low, gently convex, gradually rising from mesoscutum. Tegula unusually long (circa  $2.3\times$  as long as maximum width), posteriorly hardly narrowed, evenly curved. Propodeum with declivity finely punctured; with postero-lateral flange of median part finely imbricate, lateral lamella on each side with a few large punctures. Lateral lamella of propodeum at an angle to adjacent median part, with its outer margin gently convex, its inner margin emarginate in distal half, its apex rounded, separated from expanded postero-lateral flange of median part by narrow, sinuous, anteriorly directed slit (Fig. 22).

Terga with punctures smaller than those on thorax and with interstices micro-

sculptured yet moderately shiny; postero-lateral angles minimally produced; hind margins entire (non-crenulate).

**Male:** Both males examined are dark and similar in coloration to the southern females. The yellowish-white facial markings are slightly different from those of the female: that on the clypeus is larger, there is a marking on each arm of the frontal carina, and the marking near the eye fills the sinus rather than margining the upper inner orbit.

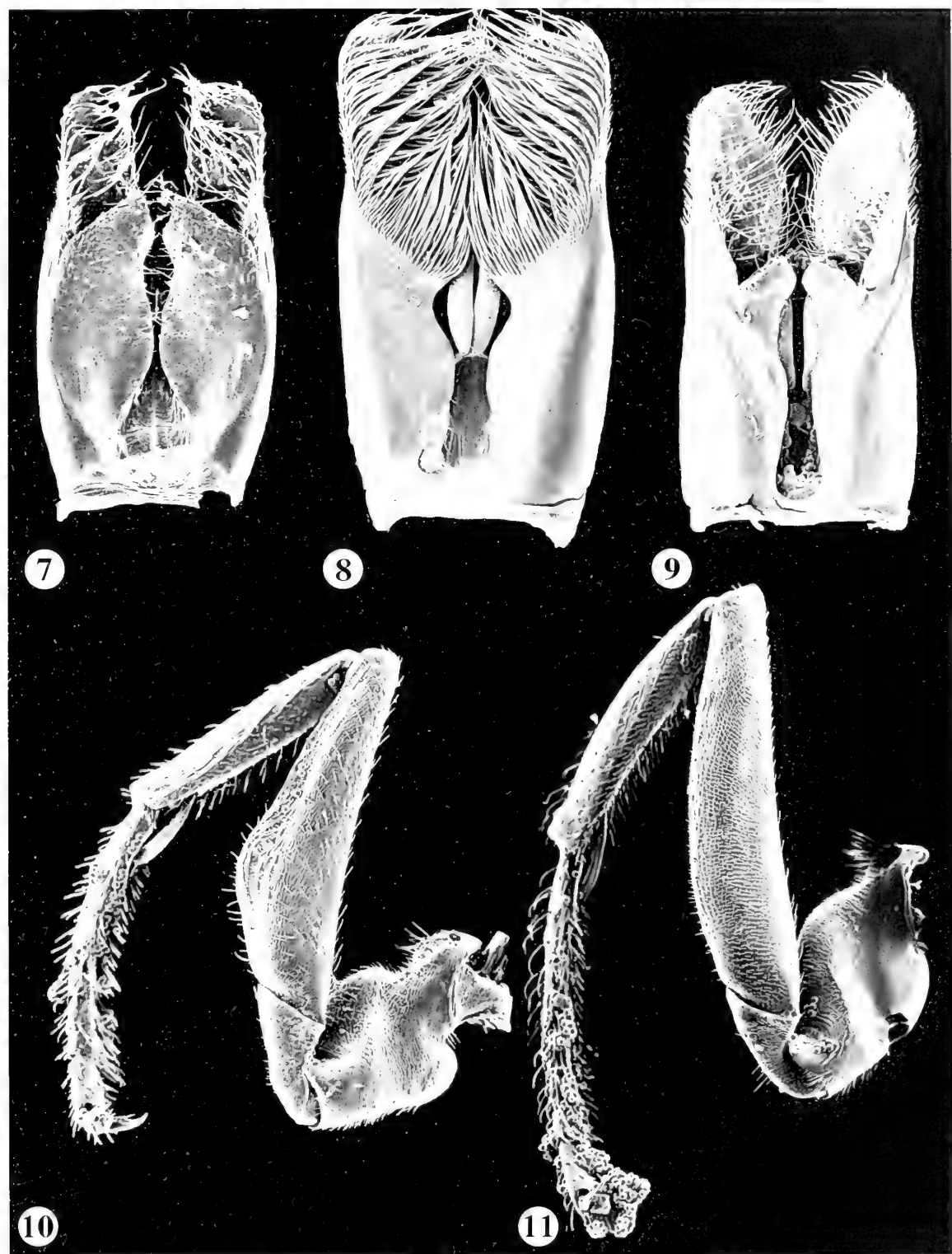
Length 7.5–7.7 mm; length of front wing 5.1–5.2 mm; hamuli 7 or 8. Length of extended tongue 5.3 mm.

More gracile than female but structurally similar, differing most noticeably in the partial effacement of the clypeal carina, the reduction of the frontal carina, the more markedly swollen antennal club and the more pronounced postero-lateral angles of the terga.

Genitalia in ventral view as in Fig. 2; in dorsal view with posterior margin of each paramere concave from rounded inner posterior angle to protruding, slightly incurved and pointed outer (lateral) posterior angle.

*Etymology.*—The name *pulcher*, a Latin adjective meaning beautiful, refers to the strikingly colourful appearance of the species.

Material examined.—Holotype: ♀, **NAMIBIA**: 57 km W of Keetmanshoop on road to Aus (26.46S 17.43E), 4.iii.2000 (F. W. and S. K. Gess) (visiting purple flowers of *Anticharis scoparia* (E. Mey. ex Benth.) Hiern ex Schinz, Scrophulariaceae) [AMG]. Paratypes: **NAMIBIA**: Two Palms, near Palmwag (19.53S 13.54E), 28.iii.2004, 1 ♀, 1 ♂ (visiting purple/violet flowers of *Anticharis inflata* Marloth & Engl., Scrophulariaceae); 120 km from Khorixas on road to Palm (20.17S 14.05E), 8.iv.1998, 6 ♀♀ (visiting purple/violet flowers of *Anticharis inflata*); 57 km W of Keetmanshoop on road to Aus (26.46S 17.43E), 4.iii.2000, 1 ♀, 1 ♂ (visiting purple flowers of *Anticharis scoparia* (E. Mey. ex Benth.) Hiern ex Schinz) – (all F.W. and S. K. Gess) [AMG].



Figs 7–11. *Celonites* species. Figs. 7–9. Ventral view of male genitalia ( $\times 50$ ). 7, *C. andrei*. 8, *C. capensis*. 9, *C. clypeatus*. Figs. 10–11 Left fore leg of female. 10, *C. heliotropii* ( $\times 50$ ). 11, *C. michaelsoni* ( $\times 40$ ).



*Geographic distribution.*—(Fig. 13): Known from northern Namibia from two localities in the Mopane Savanna of Giess (1971) and from southern Namibia from one locality in the Dwarf Desert Savanna.

*Floral associations.*—Scrophulariaceae: Aptosimeae (*Anticharis* spp.)

***Celonites kalahariensis* Gess, new species**

*Diagnosis.*—Both sexes relatively small (6.3–8.3 mm); black, with pronotum, mesopleuron, tegula, axilla, scutellum, metanotum, propodeum and gaster largely light reddish brown (male generally and in part more melanistic); clypeus and frons with carinae (that of clypeus incomplete medially and in male less pronounced than in female); sculpture (particularly in female) of frons below carina and of raised disc of clypeus (particularly below carina of each side) markedly subcostulate-punctate with raised lineations on each side running obliquely ventro-medially. Meso- and metapleura with pronounced, postero-ventrally directed, apically rounded, processes (situated below base of lateral lamella of propodeum). Male genitalia as in Fig. 4.

*Description.*—**Female:** Black. The following are yellowish white: in most specimens dorsal surface of propodeal lamella postero-laterally; ill defined and diffuse patches postero-laterally on terga I – III. The following are light reddish brown: all but extreme base of mandible; in some specimens and to a varying extent labrum, distal margin of clypeus and supracarinal marking on same, supracarinal marking on frons, narrow streak behind eyes dorsally; proximal flagellomeres and underside of club; entire pronotum; extensive area of mesopleuron; tegula; small area postero-medially on mesoscutum (in some specimens expanded to cover most of mesoscutum, in others not present); axilla; entire scutellum; metanotum; most of dorsal surface and declivity of propodeum; most of terga; underside of front femur; apex of

mid and hind femora; entire tibia and tarsi of all legs. Wings dark.

Length 6.7–8.3 mm (average of 10: 7.3 mm); length of front wing 4.3–5.3 mm (average of 10: 5.1 mm); length of extended tongue 4.4–5.8 mm (average of 3: 4.8 mm); hamuli 8 to 10 (most commonly 9).

Head  $1.3\times$  as wide as long (measured across eyes and from vertex to bottom of emargination of clypeus respectively). Clypeus below each antennal socket raised and with an inwardly curved carina (carinae not produced medially and therefore not meeting each other). Frons with well-developed, widely and shallowly V-shaped carina arising on each side opposite but outside middle of ocular sinus and meeting medially at acute angle at level of upper margin of antennal sockets. Frons above carina and vertex coarsely reticulate-punctate; frons below carina and raised disc of clypeus (particularly below carina of each side) markedly subcostulate-punctate with raised lineations on each side running obliquely ventro-medially.

Pronotum, mesopleuron, mesoscutum, scutellum and propodeum mesodorsally less coarsely sculptured than vertex, longitudinally reticulate-punctate. Scutellum rising abruptly from mesoscutum, medially somewhat swollen, slightly anteriorly produced and laterally subcarinate. Tegula circa  $1.8\times$  as long as maximum width, posteriorly narrowed with outer margin curving inwards towards rounded but acute posterior angle. Meso- and metapleura with pronounced, postero-ventrally directed, apically rounded, processes (situated below base of lateral lamella of propodeum).

Propodeum with declivity subcostulate and with lateral lamella of each side finely, closely and deeply punctured. Lateral lamella of propodeum broad, in same plane as adjacent median part, its outer margin gently curved and apex truncate, separated from median part by

narrow incurved slit (Fig. 24). Terga more finely and closely punctured than thorax; interstices microsculptured; postero-lateral angles minimally produced; hind margins entire (that is non-crenulate).

**Male:** Similar in coloration to female but generally more melanistic. Antennae entirely black; markings on head reduced, at most consisting of transverse band at base of clypeus.

Length 6.3–7.6 mm (average of 6: 6.7 mm); length of front wing 4.7–5.3 mm: 4.8 mm); length of extended tongue 4.2–5.4 mm (average of 5: 4.7 mm); hamuli 8–9 (most commonly 8).

More gracile than female but structurally similar, apart from usual more markedly swollen antennal club, less pronounced clypeal carinae, and differently formed postero-lateral angles of the terga (more produced, upwardly bent, laterally curved and apically roundly acute).

Genitalia in ventral view as in Fig. 4.

**Etymology.**—The name, a Neolatin adjective, is derived from Kalahari and is intended to indicate the provenance of the species.

**Material examined.**—Holotype: ♀, **NAMIBIA:** 71 km E of Stampriet on road to Aranos (24.09S 19.00E), 27.iii.2000 (F. W. and S. K. Gess) (visiting purple/violet flowers of *Aptosimum procumbens* (Lehm.) Steud., Scrophulariaceae) [AMG]. Paratypes: **NAMIBIA:** Gobabis [22.27S 18.58E], v.1973 (R. Bayliss), 1 ♂ [AMG]; Onse Rust 192 (24.09S 18.02E), 17–18.v.1973 [C. F. Jacot-Guillarmod), 1 ♀, 1 ♂ [AMG]; 71 km E of Stampriet on road to Aranos (24.09S 19.00E), 27.iii.2000, 1 ♀, 4 ♂♂ (visiting purple/violet flowers of *Aptosimum procumbens* (Lehm.) Steud., Scrophulariaceae); same locality, 28.iii.2000, 3 ♀♀ (1 ♀ visiting purple/violet flowers of *Aptosimum procumbens*; 1 ♀ on ground next to *Aptosimum*; 1 ♀ at hole in sand near *Aptosimum*); 24 km E of Stampriet on road to Aranos (24.14S 18.35E), 1.iv.2000, 1 ♀ (visiting purple/violet flowers of *Aptosimum procumbens*); 19 km E of Stampriet on road to Aranos (24.15S 18.33E), 1.iv.2000, 3 ♀♀, 1 ♂ (visiting purple/violet flowers of *Aptosimum procum-*

*bens*); 2 km from C17 on R511 road to Mata Mata (25.37S 19.25E), 7.iii.2000, 1 ♀ (on ground near *Aptosimum procumbens*); same locality, 8.iii.2000, 2 ♂♂ (on ground near *Aptosimum procumbens*) – (all F. W. and S. K. Gess) [all AMG]. **SOUTH AFRICA:** NORTHERN CAPE: 123 km N of turnoff from N10 on R360 from Upington to Kgalagadi Park (27.30S 20.48E), 5.iv.2000 (F. W. and S. K. Gess), 1 ♀, (visiting purple/violet flowers of *Aptosimum procumbens*) [AMG].

**Geographic distribution.**—(Fig. 14): Known only from eastern and south-eastern Namibia in the Camelthorn Savanna (Central Kalahari) and the Mixed Tree and Shrub Savanna (Southern Kalahari) of Giess (1971) and from the trans-Orange part (Gordonia) of the Northern Cape of South Africa. All collecting sites were on the red dunes of the Kalahari.

**Floral associations.**—Scrophulariaceae: Aptosimeae (*Aptosimum procumbens*).

**Discussion.**—*C. kalahariensis* is similar to *C. tumidiscutellatus* but may be distinguished by the following characters. In the female: the sculpture on the clypeus is more noticeably obliquely orientated towards the midline; the frons, midway between the V-shaped carina and the anterior ocellus is less noticeably raised; the scutellum is more abruptly and steeply raised anteriorly above the level of the mesoscutum but is less swollen medially. The distribution of reddish-brown is more extensive: notable are the frequent presence of red facial markings; the extensive red area on the mesopleuron; the entirely red scutellum; the presence of red on the propodeum; the mostly red terga; and the more extensive red on the legs.

In the male the produced postero-lateral angles of the terga are wider, more rounded and less sharply pointed apically, in consequence the hind margin of tergum VII is bi-sinuate rather than rounded. The most notable difference between the two species is in the male genitalia – compare those of *C. kalahariensis* (Fig. 4) with those of *C. tumidiscutellatus* (Fig. 5).

*Celonites arenarius* Gess, new species

*Diagnosis.*—Both sexes relatively large (7.6–10.0 mm long); black, with pronotum, tegula, terga dark reddish brown; clypeus and frons without carinae. Scutellum steeply raised anteriorly, markedly longitudinally depressed medially. Hind margins of terga markedly crenulate. Male genitalia as in Fig. 6.

*Description.*—**Female:** Black. The following are dark reddish brown: distal half of mandible; upper surface of pronotum; tegula; narrow posterior margin of scutellum; median part of metanotum; terga I and II (except for triangular black antero-medial areas); terga III and IV laterally and posteriorly; tergum V postero-medially; “knees” of all legs; underside of mid and hind tibiae and tarsi of these legs. Wings browned.

Length 8.8–10.0 mm (average of 6: 9.4 mm); length of front wing 6.6–6.8 mm (average of 4: 6.7 mm); length of extended tongue 5.4–5.8 mm (average of 2: 5.6 mm); hamuli 8 or 9.

Head 1.3× as wide as long (measured across eyes and from vertex to bottom of emargination of clypeus respectively), totally devoid of clypeal and frontal carinae. Clypeal disc convex, steeply raised laterally, with surface closely reticulate punctate and with microsculptured interstices; frons, vertex and occiput slightly more coarsely reticulate punctate. Frons slightly raised above and between antennal sockets and very slightly depressed medially above swollen area.

Pronotum, mesonotum, mesopleuron, scutellum, posterior two thirds of tegula and dorso-lateral part of propodeum somewhat more coarsely punctured than frons. Scutellum steeply raised above level of postero-medially depressed mesoscutum, medially markedly longitudinally depressed. Tegula long (circa 2.2× as long as maximum width), posteriorly narrowed with outer margin curving inwards towards rounded but acute posterior angle.

Propodeal declivity finely longitudinally rugoso-punctate. Lateral lamella of propodeum broad, its surface with large punctures and shiny interstices, its outer margin minimally curved and its apex truncate, separated from median part by an incurved slit. Terga coarsely and closely punctured; postero-lateral angles produced, acutely pointed; hind margins markedly crenulate.

**Male:** Coloration identical to that of female

Length 7.6–8.8 mm (average of 4: 8.1 mm); length of front wing 5.4–6.6 mm (average of 4: 5.8 mm); hamuli 6 to 8.

More gracile than the female but structurally similar, apart from the more markedly swollen antennal club and the more produced, very acutely pointed postero-lateral angles of the terga. Hind margins of terga even more markedly crenulate.

Genitalia in ventral view as in Fig. 6; paramere in dorsal view laterally subparallel, terminally markedly concave between produced, acutely pointed outer angle and subrightangular inner angle.

*Etymology.*—The name *arenarius*, a Latin adjective relating to sand, serves to characterize the substrate on which the species was collected.

*Material examined.*—Holotype ♀, **SOUTH AFRICA:** NORTHERN CAPE: Richtersveld, Pachtvlei [circa 7 km NE of Alexander Bay] (28.33S 16.34E), 15.ix.1996 (F. W. and S. K. Gess) (nesting in burrow in sand) [AMG]. Paratypes: **SOUTH AFRICA:** NORTHERN CAPE: Richtersveld, Pachtvlei [circa 7 km NE of Alexander Bay] (28.33S 16.34E), 15.ix.1996 (F. W. and S. K. Gess), 4 ♀♀, 4 ♂♂ (all basking on sand); same locality and collectors, 18.ix.1996, 1 ♀ (on sand) [AMG]

*Geographic distribution.*—(Fig. 15): Known only from the type locality, Pachtvlei, situated on fine wind-blown alluvial sand on the southern bank of the Orange about 7 km from its mouth.

*Floral associations.*—Unknown, no flower visiting having been observed. Pollen from

the excavated cell was identified as possibly that of *Lebeckia multiflorum* E. Mey. (Fabaceae: Papilionoideae) growing in the vicinity of the nest.

***Celonites michaelsoni* von Schulthess**

*Celonites Michaelsoni* von Schulthess, 1923: 137, male. Holotype: male, Namibia: Windhoek (Hamburg, destroyed in 1943 bombing). – Richards, 1962: 243 (speculation as to destruction of type).

*Celonites michaelsoni* von Schulthess. **Neotype**: male, Namibia: Otjitundu River, 42 km W of Okahandja (21.54S 16.31E) (AMG).

*Celonites gariensis* Gess, 1997: 41, female, male. Holotype: female, South Africa: Richtersveld National Park (AMG). **New synonym** – Gess (S. K.) et al., 1997: 75 (flower visiting, nesting); Gess and Gess, 2003: 38 (flower visiting).

*Celonites michaelsoni* von Schulthess 1923 was described from a single specimen collected by Dr W. Michaelson of the Hamburger deutsch-südwestafrikanischen Studienreise 1911 at Windhoek (now Windhoek in present day Namibia) during the period 29.iv. – 8.v.1911. The holotype, a male, was deposited in the Zoologisches Museum, Hamburg).

Richards (1962) omitted *C. michaelsoni* from his revisional study, speculating that “the type was probably at Hamburg and may well have been destroyed”. It is evident that he did not have access to any *Celonites* material from Namibia and therefore did not see any specimens answering to Schulthess’ description.

Recent collecting in Namibia, in particular that of F. W. and S. K. Gess during the period 1997–2004, has yielded a wealth of material of a common and widespread species which without any doubt is conspecific with *C. michaelsoni*. In common with some other species of wide distribution, a considerable variation is shown in the colour pattern; however, structural features, most importantly including the male genitalia, are constant across the range. The colour pattern exhibited by specimens from the north-central and

central part of Namibia, is that described by von Schulthess for the type from Windhoek.

Confirmation was received in 2005 from Dr Rudolf Abraham of the Zoologisches Museum, Hamburg that “we cannot find the type of *Celonites michaelsoni* in our collection, so it is indeed destroyed in 1943 during WW2”.

In view of the desirability of clarifying the taxonomic status of what appears to be the most common *Celonites* species occurring in Namibia, it is appropriate to designate a neotype for *C. michaelsoni*. The specimen chosen for this purpose is a male from a series of 5 ♀♀ and 3 ♂♂ from Otjitundu River, 42 km W of Okahandja (21.54S 16.31E), circa 90 km NW of Windhoek. The colour pattern is consistent with that of the destroyed holotype.

*Celonites gariensis* Gess 1997 is a synonym. The name was applied to specimens from the southern part of the species’ range, their true identity not being recognized at the time.

As already stated, *C. michaelsoni* shows a remarkable degree of colour variation across its range.

The most strikingly colored specimens, characterized by very clearly defined white lateral markings and orange-red postero-medial markings on the otherwise black terga, a white-marked black pronotum and an unmarked black mesopleuron occur in the north central part of Namibia (near Tsumeb; the Etosha National Park; between Outjo and Okaukuejo; between Omaruru and Kalkveld; between Omaruru and Karibib; and between Karibib and Okahandja).

Moving westwards there is a tendency at least for some specimens to have the terga and pronotum red rather than black but having the same markings and to have a white-marked black mesopleuron (26 km W of Kamanjab; 24 km N of Palmwag; 120 km from Khorixas on road to Palm; 40 km E of Springbokwater).

Further west still and in the Central Namib most specimens have the terga with red posterior bands which are unmarked or at most have white postero-medial markings; the pronotum and mesopleuron being generally black and unmarked (40 km E of Springbokwater; between Uis and Henties Bay; Solitaire; between Usakos and Swakopmund; Swakopmund District).

In south central and south-eastern Namibia specimens are similar to the last form but the red posterior bands have diffuse white markings both laterally and postero-medially and in some the pronotum is white marked (S. of Windhoek, Gaub bridge, E. of Hardap Dam; S. of Mariental, near Karasburg; between Karasburg and Ariamsvlei).

At the southern extremity of the species' range, that is in the Richtersveld (Northern Cape, South Africa) specimens are generally melanistic and are also somewhat smaller than those from more northern localities.

Specimens from two isolated localities in Limpopo (= Northern Province), South Africa, are similar to those from the savanna in northern Namibia.

Male genitalia in ventral view as in Fig. 3.

Material examined.—Neotype: ♂, **NAMIBIA**: Otjitundu River, 42 km W of Okahandja (21.54S 16.31E), 1 & 2.iv.2004 (F. W. and S. K. Gess) (visiting purple/violet flowers of *Aptosimum arenarium* Engl., Scrophulariaceae) [AMG]. Other specimens: **NAMIBIA**: 26 km W of Kamanjab (19.36S 14.28E), 7.iv.1998, 7 ♀♀, 2 ♂♂ (visiting purple/violet flowers of *Aptosimum angustifolium* Weber & Schinz, Scrophulariaceae); 24 km N of Palmwag (19.43S 13.51E), 18.iii.1999, 3 ♀♀ (2 visiting purple/violet flowers of *Anticharis inflata* Marloth & Engl., Scrophulariaceae; 1 visiting blue/violet flowers of *Aptosimum angustifolium*); 27 km NW of Outjo on road to Okaukuejo (19.44S 15.53E), 26.iii.1997, 1 ♂ (visiting purple flowers of *Aptosimum decumbens* Schinz); Two Palms, near Palmwag (19.53S 13.54E), 28.iii.2004, 1 ♂ (visiting white flowers of *Heliotropium tubulosum* E. Mey. ex DC., Boraginaceae); 120 km from Khorixas on road

to Palm (20.17S 14.05E), 8.iv.1998, 1 ♀, 3 ♂♂ (1 ♀ and 1 ♂ visiting purple/violet flowers of *Anticharis inflata*; 2 ♂♂ visiting white flowers of *Boerhavia deserticola* Codd, Nyctaginaceae); 40 km E of Springbokwater (20.17S 13.57E), 11.iv.2002, 2 ♀♀ (visiting violet flowers of *Anticharis inflata*); Uis to Khorixas (20.54S 15.05E), 15.iii.2004, 1 ♀ (visiting purple-violet flowers of *Anticharis*); 24 km N of Omaruru on road to Kalkveld (21.15S 16.01E), 23.iii.1997, 29 ♀♀ (28 ♀♀ visiting purple flowers of *Aptosimum arenarium* Engl.); 156 km from Khorixas, betw. Uis and Henties Bay (21.24S 14.46E), 9.iv.1998, 2 ♀♀, 1 ♂ (visiting purple/violet flowers of *Anticharis ebracteata* Schinz); 20 km S of Omaruru on road to Karibib (21.35S 15.59E), 23 and 24.iii.1997, 5 ♀♀, 1 ♂ (3 ♀♀ visiting purple flowers of *Aptosimum arenarium*; 2 ♀♀, 1 ♂ on ground next to this plant); 30 km S of Omaruru on road to Karibib (21.41S 15.59E), 26.iv.2002, 5 ♀♀, 3 ♂♂ (visiting bluish violet flowers of *Aptosimum arenarium*); Karibib to Omaruru (21.51S 15.55E), 12.iii.2004, 1 ♂; Otjitundu River, 42 km W of Okahandja (21.54S 16.31E), 1 & 2.iv.2004, 5 ♀♀, 2 ♂♂ (visiting purple/violet flowers of *Aptosimum arenarium*); 72 km E of Karibib on road to Okahandja (21.54S 16.31E), 1.iv.1998, 1 ♀, 2 ♂♂ (visiting purple flowers of *Aptosimum arenarium*); 94 km E of Karibib on road to Okahandja (21.57S 16.43E), 1.iv.1998, 1 ♀ (visiting purple/violet flowers of *Aptosimum arenarium*); 77 km E of Henties Bay on road to Klein Spitzkuppe (21.54S 14.58E), 19.iv.2002, 1 ♀ (visiting white flowers of *Heliotropium tubulosum*); 58 km SW of Usakos on road to Swakopmund (22.12S 15.10E), 23.iv.2002, 2 ♀♀ (1 ♀ visiting violet flowers of *Aptosimum spinescens* (Thunb.) Weber; 1 ♀ on ground next to this plant); 7 km from Gaub bridge towards Kuiseb River (23.27S 15.48E), 14.iv.1998, 7 ♀♀ (visiting purple/violet flowers of *Aptosimum lineare* Marloth & Engl.); Solitaire (23.52S 16.00E), 30.iv.2002, 3 ♀♀, 2 ♂♂ (visiting purple/violet flowers of *Aptosimum spinescens*); E of Hardap Dam (24.29S 17.53E), 4.iv.1997, 1 ♀, 1 ♂ (visiting purple flowers of *Aptosimum glandulosum* Weber & Schinz); 25 km S of Mariental (24.50S 17.56E), 16.iv.1998, 2 ♀♀ (visiting purple/violet flowers of *Aptosimum spinescens*); S of Maltahöhe on D811 (25.16S 17.03E), 23.iii.1999, 1 ♂ (visiting purple/violet flowers of *Aptosimum spinescens*); Klein-Aus-Vista (26.41S 16.13E), 23.ix.2003, 4 ♀♀, 3 ♂♂ (visiting purplish violet flowers of *Aptosi-*



*num tragacanthoides* E. Mey. ex Benth.); circa 3 km NNW of Karasburg (27.58S 18.43E), 6.iii.1999, 1 ♀ (visiting purple flowers of *Aptosimum spinescens*); between Karasburg and Ariamsvlei (28.05S 19.25E), 18.iv.1998, 1 ♀ (ex nest) – (all F. W. and S. K. Gess) [all AMG]; 10 km SE of Tsumeb [19.17S 17.48E], 8.iii.1990, 1 ♂; 62 km E of Karibib [21.53S 16.25E], 20.ii.1990, 1 ♀, 4 ♂♂; 17 km W of Okahandja [21.57S 16.44E], 19.ii.1990, 1 ♂; 28 km S of Windhoek [22.49S 17.08E], 17.ii.1990, 2 ♂♂ – (all W. J. Pulawski) [all CAS]; Etosha Nat.Park, Nau-Obes (19.19S 16.37E), 17.i.1987 (J. Irish, E. Marais) 2 ♀♀; Damaraland, 6 km N Arandis (22.22S 14.59E), 1.iii.– 9.iv.1985, 1 ♀, 9.iv.– 6.v.1985, 1 ♀ (both J. Irish, H. Rust); Swakopmund Dist., Rössing Mine (22.28S 15.02E), 8.v.– 5.vi.1984 (J. Irish, H. Liessner), 1 ♀; Swakopmund Dist., Lower Ostrich Gorge (22.30S 14.58E), 5.vi.– 3.vii.1984 (J. Irish, H. Liessner), 1 ♀; Hoogland 132, Maltahöhe (SE2416Cd) [24.45S 16.15E], 1–3.ii.1974, 1 ♀; Vogelstrausskluff 87, Bethanien (SE2717Ba) [27.00S 17.31E], 24–29.ix.1974 (? collector), 1 ♂ – [all NNIC]. **SOUTH AFRICA:** LIMPOPO (formerly NORTHERN PROVINCE): Louis Trichardt (2239BB sic!!) [23.03S 29.55E], 27.vi.1991 (M. Lorenz), 1 ♀; Rust de Winter Dam [25.15S 28.29E], 12.x.1980 (F. J. Herbst), 1 ♀, 1 ♂ [all AMG]; NORTHERN CAPE: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S 17.03E), 17–21 and 24.ix.1995, holotype ♀, 33 paratype ♀♀, 4 paratype ♂♂ of *C. garipeensis* Gess (33 ♀♀ incl.holotype, 3 ♂♂ in deep violet flowers of *Peliostomum* sp., Scrophulariaceae; 1 ♀, 1 ♂ in purple-violet flowers of *Aptosimum spinescens*); same locality, 6.ix.1996, 1 paratype ♀, 7 paratype ♂♂ of *C. garipeensis* (♀, 6 ♂♂ on ground near flowering *Peliostomum* sp.); Namaqualand, Richtersveld National Park, Paradise Kloof (28.19S 17.01E), 22.ix.1995, 1 paratype ♀ of *C. garipeensis* (associated with nest); Namaqualand, Richtersveld National Park, 1.5 km from Helskloof gate (28.18S 16.57E), 8 and 9.ix.1996, 3 paratype ♀♀, 1 paratype ♂ of *C. garipeensis* (all on ground near *Aptosimum spinescens*) – (all F. W., S. K. and R. W. Gess) [all AMG].

**Geographic distribution.**—(Fig. 16): Known in Namibia from collection localities spanning ten degrees of latitude in the Mopane Savanna, Saline Desert with Dwarf Scrub Savanna Fringe, Mountain Savanna and Karstveld, Thornbush Savanna, Central Namib, Semi-desert and Savanna Transi-

tion, Highland Savanna, and Dwarf Scrub Savanna of Giess (1971). In South Africa it is known from the Richtersveld National Park (Northern Cape) in the Namaqualand Broken Veld of Acocks (1953) and from two localities in Limpopo in the Mixed Bushveld of Acocks.

**Floral associations.**—Scrophulariaceae: Aptosimeae (*Anticharis* spp., *Aptosimum* spp., *Peliostomum* sp.).

### Known species of *Celonites* not previously recorded from Namibia.

#### *Celonites andrei* Brauns

*Celonites andrei* Brauns, 1905: 228, female. Holotype: female, South Africa : Willowmore (TMP). – Brauns, 1913: 206, male, female, nest; Richards, 1962: 236 (revision); Gess, 1996: 222 (flower visiting); Gess and Gess, 2003: 36 (flower visiting).

#### Male genitalia (Fig. 7)

**Material examined.**—**NAMIBIA:** Sperrgebiet (Diamond Area 1): Tsaukhaib (26.43S 15.40E), 13 and 15.ix.2005 (F. W. and S. K. Gess), 1 ♀, 2 ♂♂ (both sexes associated with *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae, flying around plants, alighting on ground next to them, ♀ observed entering a flower).

**Geographic distribution.**—(Fig. 17): Known in Namibia from a single locality on the old wagon track from Lüderitz to Aus, in the north of Diamond Area 1 in the Desert and Succulent Steppe (Winter rainfall area) of Giess (1971). It is widely distributed in the Karoo Biome of South Africa, specimens in the Albany Museum collection being from the Northern Cape (Twee Rivieren in the Kalahari Gemsbok National Park, the Richtersveld National Park, Anenous, Springbok, and near Norvalspont), from the Western Cape (near Prince Albert) and from the Eastern Cape (Steytlerville).

In South Africa, as in Namibia, the species has been recorded visiting flowers solely of Scrophulariaceae: Aptosimeae (*Aptosimum procumbens* (Lehm.) Steud., *A.*



Figs 12–17. *Celonites* species. Distributions. 12, *C. heliotropii*. 13, *C. pulcher*. 14, *C. kalahariensis*. 15, *C. arenarius*. 16, *C. michaelsoni*. 17, *C. andrei*.

*spinescens* (Thunb.) Weber, and *Peliostomum virgatum* E. Mey. ex Benth.)

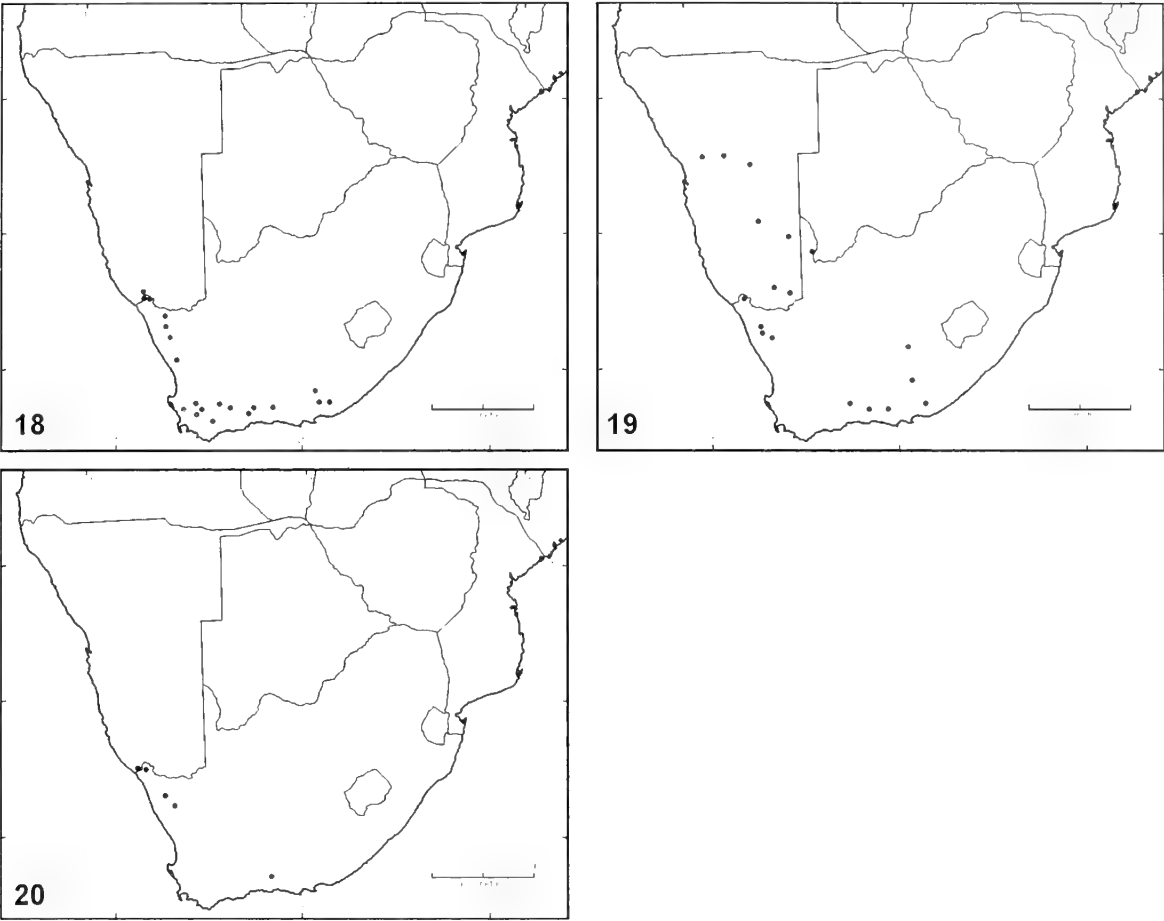
*Celonites capensis* Brauns

*Celonites capensis* Brauns, 1905: 231, female. Holotype: South Africa: Willowmore (TMP). –

Brauns, 1913: 205, male; Richards: 1962: 235 (revision); Gess, 1996: 223 (flower visiting); Gess and Gess, 2003: 37 (flower visiting).

Male genitalia (Fig. 8)

Material examined.—**NAMIBIA**: 16 km S of Rosh Pinah (28.04S 16.51E), 13–15.x.2000, 24 ♀♀



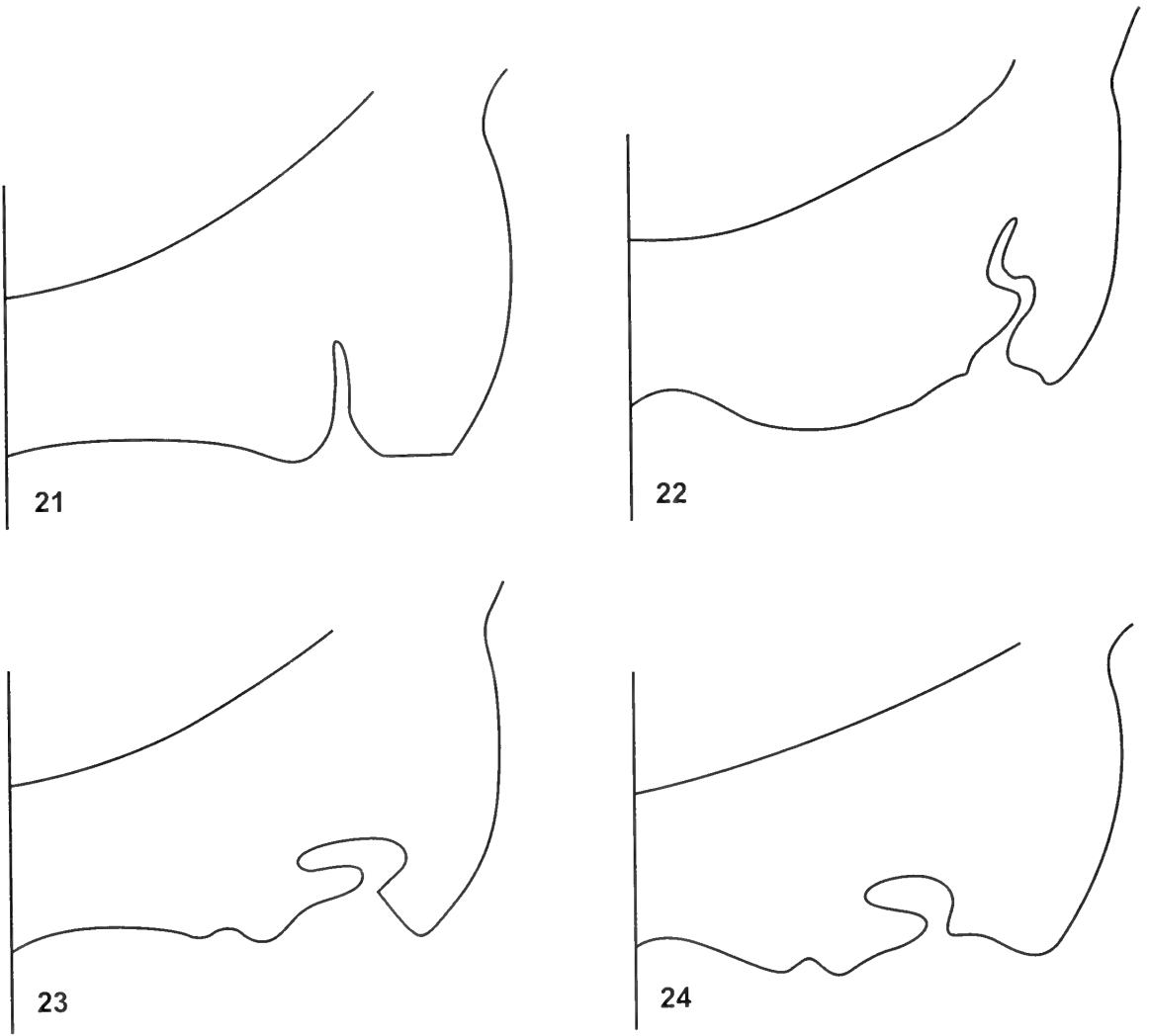
Figs 18–20. *Celonites* species. Distributions. 18, *C. capensis*. 19, *C. clypeatus*. 20, *C. tumidiscutellatus*.

(14 ♀♀ visiting yellow flowers of *Tripteris microcarpa* Harv., Asteraceae; 3 ♀♀ visiting yellow flowers of *Gazania lichtensteinii* Less., Asteraceae; 3 ♀♀ visiting yellow flowers of *Didelta carnosa* (L.f.) Ait., Asteraceae; 4 ♀♀ visiting pinkish white flowers of Aizoaceae: *Mesembryanthema*) – (all F. W. and S. K. Gess) [all AMG]; Diamond Area 1, Daberas (28.12S 16.49E), 14–29.ix.1994 (E. Marais) 1 ♀ (Pres. pitf. traps) [NNIC].

*Geographic distribution*.—(Fig. 18): Known in Namibia from two closely adjacent localities in the extreme south of the Desert and Succulent Steppe (Winter rainfall area) of Giess (1971). It is widely distributed in the Karoo Biome of South Africa, specimens, mostly in the Albany Museum collection, being from the Northern Cape (Richterveld, between Vioolsdrif and Springbok, Voëlklip near Springbok, and Sors Sors near Kamie-

skroon), from the Western Cape (Nuwerus, near Ceres, Malmesbury, Ladismith, and near Oudtshoorn) and from the Eastern Cape (several localities near Grahamstown). Richards (1962) recorded the species from Worcester, Montagu and Matjesfontein in the Western Cape and from Willowmore and Somerset East in the Eastern Cape.

In South Africa the species has been recorded visiting the flowers of a wide range of plants: Asteraceae (*Berkheya* spp., incl. *Berkheya heterophylla* (Thunb.) O. Hoffm., and *Senecio pterophorus* DC.), Aizoaceae: *Mesembryanthema* (*Drosanthemum* sp. and *Prenia pallens* (Ait.) N. E. Br.), Geraniaceae (*Pelargonium myrrhifolium* (L.) L'Hérit.), Scrophulariaceae (*Phyllopodium cuneifolium* (L. f.) Benth.), Campanulaceae (*Wahlenbergia ecklonii* Buek), Irida-



Figs 21–24. *Celonites* species. Diagrammatic representations of postero-lateral part of propodeum. 21, *C. capensis*. 22, *C. pulcher*. 23, *C. michaelsoni*. 24, *C. kalahariensis*.

ceae (*Ferraria* sp.), and Boraginaceae (*Ehretia rigida* (Thunb.) Druce).

### *Celonites clypeatus* Brauns

*Celonites clypeatus* Brauns, 1913: 206, female. Holotype: South Africa: Willowmore (TMP). – Richards, 1962: 236 (revision); Gess, 1996: 223 (flower visiting); Gess and Gess, 2003: 38 (flower visiting).

#### Male genitalia (Fig. 9)

Material examined.—**NAMIBIA**: 62 km E of Karibib [21.53S 16.25E], 20.ii.1990 (W. J. Pulawski), 3 ♀♀ [CAS]; 10 km W of Usakos on road to Swakopmund (21.59S 15.30E), 12 &

13.iii.2004, (F. W. and S. K. Gess), 2 ♀♀, 3 ♂♂ (visiting purple violet flowers of *Aptosimum arenarium* Engl., Scrophulariaceae) [AMG]; Excelsior 206, Windhoek (22.27S 17.38E), 1–31.viii.1979 (S. Louw, M.-L. Penrith), 1 ♂ [NNIC]; 25 km S of Mariental (24.50S 17.56E), 16.iv.1998, 3 ♀♀, 1 ♂ (visiting purple/violet flowers of *Aptosimum spinescens* (Thunb.) Weber); 2 km from C17 on R511 road to Mata Mata (25.37S 19.25E), 8.iii.2000, 1 ♀; circa 3 km NNW of Karasburg (27.58S 18.43E), 6.iii.1999, 2 ♀♀ (visiting purple flowers of *Aptosimum spinescens*); between Karasburg and Ariamsvlei (28.05S 19.25E), 18.iv.1998, 1 ♀ (visiting purple/violet flowers of *Aptosimum spinescens*) - (all F. W. and S. K. Gess) [all AMG];

*Geographic distribution*.—(Fig. 19): Known in Namibia from collection localities spanning seven degrees of latitude in the southern half of the country in the Thornbush Savanna, the Highland Savanna, and the Dwarf Scrub Savanna of Giess (1971). It is widely distributed in the Karoo Biome of South Africa, specimens in the Albany Museum collection being from the Northern Cape (Twee Rivieren in the Kalahari Gemsbok National Park, the Richtersveld National Park, Springbok, Leliefontein and near Norvalspont), from the Western Cape (near Prince Albert) and from the Eastern Cape (between Cradock and Hofmeyr, Grahams-town, Steytlerville and Willowmore).

In South Africa, as in Namibia, the species has been recorded visiting the flowers solely of Scrophulariaceae: *Aptosimeae* (*Aptosimum indivisum* Burch., *A. procumbens* (Lehm.) Steud., *A. spinescens* (Thunb.) Weber, and *Peliostomum virgatum* E. Mey. ex Benth.)

*Celonites tumidiscutellatus* Gess

*Celonites tumidiscutellatus* Gess, 1997: 44, female, male. Holotype: female, South Africa, [Northern Cape Province,] Namaqualand, Springbok, Hester Malan [now Goegap] Nature Reserve (AMG). – S. K. Gess et al., 1997: 76

(flower visiting); Gess and Gess, 2003: 40 (flower visiting).

Male genitalia (Fig. 5)

Material examined.—**NAMIBIA**: E of Oranjemund, 37 km from checkpoint on road to Sendelingsdrif (28.23S 16.44E), 24.ix.1997, 4 ♀♀ (visiting purple/violet flowers of *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae); E of Oranjemund, 28 km from checkpoint on road to Sendelingsdrif (28.26S 16.42E), 25.ix.1997, 2 ♀♀, 1 ♂ (visiting violet flowers of *Peliostomum leucorrhizum* E. Mey. ex Benth., Scrophulariaceae) – (all F. W. and S. K. Gess) [all AMG].

*Geographic distribution*.—(Fig. 20): Known in Namibia from the northern bank of the Orange in the extreme south of the Desert and Succulent Steppe (Winter rainfall area) of Giess (1971). In South Africa it is known from the Northern Cape (Richtersveld National Park , near Springbok and Leliefontein) and from the Eastern Cape (Willowmore).

In South Africa, as in Namibia, the species has been recorded visiting the flowers solely of Scrophulariaceae: *Aptosimeae* (*Aptosimum indivisum* Burch., *A. procumbens* (Lehm.) Steud., *A. spinescens* (Thunb.) Weber, and *Peliostomum virgatum* E. Mey. ex Benth.)

KEY TO SPECIES OCCURRING IN NAMIBIA

1. Propodeum postero-laterally with long, anteriorly directed slit separating off lateral lamella from medial part of propodeum; slit straight or sinuous, not or only minimally incurved anteriorly (Figs 21, 22) ..... 2
- Propodeum postero-laterally with anteriorly directed slit which after very short distance is incurved and ends in circular emargination or extends medially in transverse direction, in both conditions cutting off lateral lamella leaving part of hind margin of median part of propodeum as narrow finger-like process pointing towards end of lateral lamella (Figs 23, 24) ..... 3
2. Propodeal slit narrow and straight (Fig. 21); lateral lamella distally broadly truncate, more or less in same plane as adjacent median part of propodeum. Neither clypeus nor frons with carina (though frons may have low swelling). Male genitalia: Fig. 8 ..... *capensis* Brauns
- Propodeal slit narrow and sinuous (Fig. 22); lateral lamella distally narrowly and obliquely truncate, at angle to adjacent median part of propodeum; median part of propodeum postero-laterally markedly produced, lamellate (Fig. 22). Both clypeus and frons with carina (though clypeal carina may be weak or absent in male).

Clypeus and frons shiny, with small, well separated punctures and smooth interstices; mesoscutum and scutellum markedly longitudinally reticulate-punctate. Male genitalia: Fig. 2 ..... *pulcher* Gess n. sp.

3.	Frons with V-shaped carina (sometimes weak medially); clypeus with an M-shaped carina (if medially weak and diffuse, at least well developed laterally) .....	4
-	Frons without a V-shaped carina .....	8
4.	Meso- and metapleura with pronounced, postero-ventrally directed, apically rounded, processes (situated below base of lateral lamella of propodeum). Pronotum, mesopleuron, tegula, axilla, scutellum, metanotum, propodeum and gaster largely red. In some specimens (particularly females) clypeus baso-medially and frons supra-carinally with transverse red markings. Male genitalia: Fig. 4. ....	<i>kalahariensis</i> Gess n. sp.
-	Meso- and metapleura without such processes .....	5
5.	Mesopleuron with variously sized (to minute) red marking .....	6
-	Mesopleuron either totally black or with white marking .....	7
6.	Frons with small red (or yellow) spot on each side [in female situated next to upper margin of ocular sinus, that is, above carina; in male situated within lower half of ocular sinus, that is, below carina]. Clypeus of female occasionally with red spot, that of male usually with red or yellow spot. Carinae on frons and clypeus of female poorly developed medially, those of male even more poorly developed and almost effaced respectively. Scutellum falling abruptly onto mesoscutum (especially in female). Male genitalia: Fig. 7 .....	<i>andrei</i> Brauns
-	Frons without small red spot on each side in female but in male occasionally with red spot within lower half of ocular sinus. Clypeus of both sexes immaculate. Carinae on frons and clypeus of female well developed throughout, both carinae less developed but indicated in male. Scutellum falling gradually onto mesoscutum. Male genitalia: Fig. 9 .....	<i>clypeatus</i> Brauns
7.	Frons, clypeus and mesopleuron totally black, dorsal part of pronotum red, abdominal terga black with reddish posterior bands; scutellum medially raised (subconical) and anteriorly falling gradually onto mesoscutum (see Gess 1997: Fig. 9). Male genitalia: Fig. 5 .....	<i>tumidiscutellatus</i> Gess
-	Frons, clypeus and mesopleuron often with white spots, dorsal part of pronotum black with white humeral spots and white or yellow (to orange) hind margin, abdominal terga with reddish posterior bands and white lateral and medial spots; scutellum antero-medially almost overhanging mesoscutum and falling very abruptly onto it (see Gess 1997: Fig. 3). Male genitalia: Fig. 3 (See also Gess 1997: Figs 5 and 6) .....	<i>michaelseni</i> von Schulthess
8.	Fore femur (more particularly that of female) produced postero-ventrally in proximal half (Fig. 10). Pronotum, tegula, scutellum and posterior bands on terga red. Male with most of mandibles, entire labrum and clypeus and variably developed facial markings lemon yellow. Male genitalia: Fig. 1 .....	<i>heliotropii</i> Gess n. sp.
-	Fore femur unmodified. Hind margins of terga very markedly crenulate. Scutellum steeply raised anteriorly, markedly longitudinally depressed medially. Pronotum, tegula and terga (largely) red. Pale facial markings absent. Male genitalia: Fig. 6 .....	<i>arenarius</i> Gess n. sp

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## Notes on Nesting and Flower Visiting of some Anthidiine Bees (Hymenoptera: Megachilidae: Megachilinae: Anthidiini) in Southern Africa

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*Abstract.*—For Anthidiini occurring in southern Africa, descriptive notes on nests of seven species belonging to three genera, have been published. All are constructed from plant fibres and, depending upon the species, are situated aerially on plants or in pre-existing cavities. To these are added first descriptions of nests of three further species representing three genera. *Serapista rufipes* (Fries), like the only other species of *Serapista*, *S. denticulata* (Smith), for which nesting is known, was found to construct nests from plant fibres, however, although similarly found aerially on plant stems, a nest with its builder was discovered in a burrow in the ground. *Afranthidium* (*Nigranthidium*) *concolor* (Fries) was found nesting in a burrow in the ground, like other species of *Afranthidium*, using plant fibres. *Plesianthidium*, represented by *P. (Spinanthidiellum) volkmanni* (Fries), was found constructing groups of separate resinous, spouted, pot-like cells, similar to those constructed by some extraterritorial species of *Anthidiellum*. Additional nest records are given for *Afranthidium* (*Immanthidium*) *repetitum* and *Afranthidium* (*Afranthidium*) *ablusum*. A first record (that of Alan Weaving) of a host, *Megachile* (*Gronocerus*) *feline* Gerstaecker, of *Euaspis abdominalis* (Fabricius) is reported. Anthidiini in southern Africa are relatively polyphagous. In the present analysis inter-generic and intra-generic similarities, differences, and preferences in flower families visited are indicated.

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Anthidiini are worldwide in distribution. Michener (2000) recognizes 37 genera of which 18 are represented in Africa south of the Sahara - 15 in southern Africa. Anthidiine bees are generally divisible into two groups on the basis of the materials used for nest construction. One group uses plant hairs or plant fibres and the other resin, often together with pebbles (Michener 1968, Pasteels 1977, Michener 2000). However, *Pachyanthidium bicolor* (Lepeletier) is exceptional as it uses a mixture of plant down and resin (Michener 1968, 2000).

Surprisingly little has been published on the nesting of anthidiine bees in southern Africa. Nesting records are available for seven species from three genera, all using plant fibres: *Afranthidium* (*Immanthidium*)

*junodi* (Fries) (as *Anthidium junodi* Fries - Skaife 1950, Taylor 1962, Michener 1968 and as *Immanthidium junodi* (Fries) - Gess 1981); *Afranthidium* (*Immanthidium*) *repetitum* (Schulz) (as *Anthidium repetitum* Schulz - Michener 1968); *Afranthidium* (*Branthidium*) *micrurum* (Cockerell) (as *Anthidium micrurum* Cockerell - Michener 1968); *Afranthidium* (*Branthidium*) *braunsi* (Fries) (as *Branthidium braunsi* - Gess 1981); *Afranthidium* (*Afranthidium*) *ablusum* (Cockerell) (as *Afranthidium* (*Oranthidium*) probably *odonturum* (Cockerell) (Gess and Gess 1999); *Pseudoanthidium* (*Micranthidium*) *truncatum* (Smith) (as *Micranthidium truncatum* Smith - Fries 1902, Michener 1968); *Serapista denticulata* (Smith) (Stadelmann 1898, quoted by Fries 1905, 1909, 1916, Michener 1968).

To these published records are added first descriptions of the nests of *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friese), a resin user, and of *Serapista rufipes* (Friese) and *Afranthidium* (*Nigranthidium*) *concolor* (Friese), plant fibre users, additional records for *Afranthidium* (*Immanthidium*) *repetitum* and *Afranthidium* (*Afranthidium*) *ablusum*, and a first record (that of Alan Weaving) of a host of *Euaspis abdominalis* (Fabricius).

Although provision from the nests was not investigated, flowers visited are discussed based on the records assembled for 13 of the 15 genera known from southern Africa. The two genera not represented are parasitic in the nests of other bees and therefore visit flowers only for adult nourishment and egg production. In a comparative overview of flower visiting by non-*Apis* bees in the semi-arid to arid areas of southern Africa (Gess and Gess 2004) the authors compared diversity of choice between and within bee families, in the case of Megachilidae to the level of sub-tribe, but no comparisons were made within sub-tribes. The present contribution, restricted to Anthidiini, examines flower visiting at inter- and intra-generic levels.

## METHODS

Nests of anthidiines have been rarely encountered by the authors and no full nesting studies were conducted by them. The notes on nesting are limited to a small number of opportunistic observations and collections. Voucher specimens of the bees and of their nests have been deposited in the insect collection of the Albany Museum.

Field research by the authors, spanning 35 years, has been concentrated principally within the Karoo Biome and associated dry savanna, dry fynbos and desert. Apart from in the area around Grahamstown in the Eastern Cape where the authors reside it has not been possible to work in the field throughout the year. In the southeast and south peaks of rainfall are in September

and March and the summer is rarely excessively hot and dry. Thus, in these areas, sampling has been principally from late October through to March. In the winter rainfall region of the southwest, north to Lüderitz and Aus in southwestern Namibia, sampling has been from August, when temperatures start to rise, through to December, when most flowering is over and the land as a general rule becomes parched. North of the Orange River in the southern Kalahari, southeastern Namibia and in western Namibia to the north of the winter rainfall area, sampling has been in March and April, which is when rains are expected and excessive heat is past.

Insects visiting flowers were collected using a hand net. All plants in flower at the study site were observed for visitors and, when possible, were sampled throughout the day. In effect anthidiine bees in an area all had the choice of visiting all those plants that were in flower. Records encompass both types of visit, for collecting nectar and for collecting pollen, indiscriminately.

The records used in the present analysis are listed in the Appendix. Except where indicated, they are condensed from the authors' collection labels. Many of the specimens were collected after the catalogue (Gess and Gess 2003) and the electronic bee database were closed in March 2002. Full locality data, including co-ordinates, and exact dates of all specimens are available from label data and of those for specimens processed before March 2002 in addition from the electronic, relational database.

The great majority of records relate to specimens in the terrestrial insect collection of the Albany Museum, Grahamstown. Voucher specimens for many but not all plants have been deposited in the Schönland Herbarium, Albany Museum, Grahamstown. Duplicates of specimens from Namibia are in the National Herbarium of Namibia, Windhoek. A few additional records have been added from literature

and from specimens collected by V. Whitehead, determined by C.D. Michener and deposited in the collection of the South African Museum, Cape Town (see Appendix). The records listed in Struck (1994) have not been included because it is not clear whether "the flower visiting records .. compiled from direct field observations" are supported by voucher specimens.

The value of including single records of visits to a particular plant family by a particular species of bee have been questioned. Taken singly such records are of little value but taken together with records for other species they are of value in indicating plant families visited by bees at higher taxonomic levels.

Specific flower visitors show varying degrees of diversity of choice, i.e. of oligophagy and polyphagy. In order to make comparisons between groups of flower visitors constituted of unequal numbers of species Gess (1992, unpublished) developed an Index of Diversity of Choice at the specific level, using the formula:

$$D = a-b/b \times 100$$

where  $a$  = the sum of the number of species recorded visiting each of the flower families and  $b$  = the number of species of flower visitors (published in Gess 1996 page 47). This is an index by which to compare the degree of oligophagy or polyphagy exhibited by taxa of differing numbers of species. 'D' would equal 0 if each species only visited one species of plant; the higher the value of 'D' the greater the degree of polyphagy.

## NEW NEST RECORDS

### *Plesianthidium* Cameron

*Plesianthidium* consists of four sub-genera, *Carinanthidium* Pasteels, *Plesianthidium* Cameron, *Spinanthidiellum* Pasteels, and *Spinanthidium* Mavromoustakis known from South Africa only, principally from the west (Michener 2000)

*Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Fries) was found nesting abundantly in electricity boxes placed 1.25 m above the ground, provided for campers in the Clanwilliam Dam Resort, Olifants River Valley (Figs 1, 2). Sixty-nine electricity boxes were inspected. Of these 24 had been used for nesting by *P. (S.) volkmanni*.

Within these pre-existing cavities clusters of up to seven separate spouted, pot-like cells with resinous walls had been constructed. The cells were attached horizontally to a wall of the cavity or horizontally on the floor of the cavity (Fig. 3). All of the cells within a cavity were orientated in the same direction but there was no constancy between cavities. In no cases was there more than one cell under construction, suggesting that each cluster had been constructed by a single female.

Construction of a cell was in all cases preceded by the construction of a small "pad or saucer", noticeably different in texture from the cell walls, and attached to the substrate. The cell was then constructed on this base. When a cell had been only partially constructed, at the close of day, the female slept head down within the cell with her gaster curved over within the cell so that only the arched terga were exposed (Fig. 4).

Measurements were taken from a sample of 13 cells (deposited in the collection of the Albany Museum). The average total length is 14.9 mm including the spout. The cell without the spout is 11 mm in length and 7.7 mm in diameter. The walls of the cells are circa 0.5 mm in thickness and the diameter of the opening of the spout at the tip circa 0.5 – 1 mm. The channel within the spout is filled with very short lengths of fine plant material, not fibres or "fluff". The resinous walls are yellow ochre in colour, initially smooth and pliable. When under construction the walls of the wide portion of the cell are made higher than the final height of the cell-proper. The edges are then crimped to



Fig. 1. Vegetation on the eastern side of the Clanwilliam Dam, Olifants River Valley, Western Cape.

Fig. 2. Electricity box in the caravan park on the eastern side of the Clanwilliam Dam.

Fig. 3. Cells of *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friesse) constructed inside an electricity box. Note: initial "pad or saucer" on which a cell is constructed, partially constructed cell and five completed cells, three attached to the vertical wall and one to the floor. Average actual length of cells 14.9 mm including spout.

Fig. 4. Two cells of *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friesse) constructed inside an electricity box. Note nest builder sleeping in the incomplete cell.

form the top of the cell-proper but not reaching the centre, construction then continues with a gentle narrowing of the tube of the spout.

Provisioning takes place before crimping and spout construction. Provision taken from a cell (Fig. 5) appeared to be of mixed provenance with an admixture of bright yellow oil. Pollen from the flowers of *Aspalathus spinescens*, the only flowers from which these bees were collected in the vicinity of the nests, is represented mixed with bright yellow oil. The completed provision filled circa 2/3 of the cell-proper.

The resinous walls are probably impervious to air. The function of the spout is most probably for ventilation.

The cocoon is attached to the inner surface of the wall of the cell-proper with the papilla within the base of the spout. Silken threads are visible within the brittle, highly varnished, brown walls of the cocoon.

Emergence from the cocoon is through the side of the cell-proper, a large exit hole being cut by the emerging adult (Fig. 6).

There was a high level of success, *P. (S.) volkmanni* having emerged from most of the circa 20 cells collected. However, a meloid larva emerged from one of the cells and pupated attached to the outside of the cell (Fig. 7).

### *Serapista* Cockerell

The Afrotropical genus *Serapista* Cockerell consists of four species, two of which are represented in southern Africa – the widespread *S. denticulata* (Smith) recorded from central, eastern and southern Africa and the more restricted *S. rufipes* (Friese) recorded only from southern Africa (Pastes, 1984).

Published data concerning the nests of *Serapista* all appear to apply to *S. denticulata* Smith (Stadelmann, 1898, quoted by Friese, 1905 and 1909, Friese 1916, Michener 1968, with republication of his Figs 27-28 by Roubik 1989, Michener, 2000). Michener (1968) illustrated and gave a full descrip-



Fig. 5. Cell of *Plesianthidium (Spinanthidiellum) volkmanni* (Friese) cut through longitudinally to show provision and young larva.

Fig. 6. Cell of *Plesianthidium (Spinanthidiellum) volkmanni* (Friese) showing emergence hole and imago.

Fig. 7. Cell of *Plesianthidium (Spinanthidiellum) volkmanni* (Friese) from which a meloid beetle emerged, showing pupal skin of and adult of the beetle.

tion of a nest from Malawi, commented on further nests in the British Museum from Natal, and summarized the accounts of the earlier authors. However, the assumption has been made that the form of the nest of *S. denticulata* and its aerial situation holds

good also for the other species of the genus. Thus it is stated by Michener (1968) that "bees of this genus make exposed nests of down" and by Michener (2000), with regard to the genus, that "nests, masses of plant down often intermixed with animal hairs or even feathers and placed on plant stems have been described by several authors..."

In the Albany Museum, collected by the present authors in the vicinity of Grahamstown, Eastern Cape (Fig. 8), are two nests of *S. denticulata* (Figs 9, 10), identified as such from, in one instance, the capture of the builder and, in both from the bees reared from them (a female and a male from one and eight females and three males from the other). Additional identified typical nests of this species are two in a public display in the Albany Museum and others held in the collection of the South African Museum (Margie Cochran pers. com.). Typical nests are roughly oval in shape with a short entrance tube at the higher end.

The four Grahamstown nests like those described in literature are aerial nests built on shrubs, the recorded height above ground of one being circa 50 cm. Two consist entirely of plant down, the other two in patches incorporate fine gray mammalian fur. The nests illustrated are 76 mm and 70 mm in height and 29 mm and 50 mm in diameter respectively. They were constructed on stems of *Elytropappus* (Asteraceae) and *Rhus* (Anacardiaceae). From a third nest, similar in construction and placement, collected by W.A. Clarke from *Lebeckia* (Fabaceae: Papilionoideae) near Twee Rivieren, Gemsbok National Park in 1966 (Figs 11, 12), were reared four female and three male *Serapista rufipes* Friese (nest and bees in the collection of the Albany Museum), supporting the belief that *Serapista* constructs only aerial nests. This nest was similar in size, 72 mm in height and 43 mm in diameter.

The authors sampled bees visiting flowers throughout the semi-arid to arid areas

of southern Africa (Gess and Gess 2004). Although *Serapista rufipes* was commonly encountered and observed throughout the south-western areas of South Africa and widely in Namibia, no further nests were found, nor were nests found in the collections of the South African Museum (Margie Cochran pers. com.) nor in the National Collection, PPRI, Pretoria (Connal Eardley pers. com.), both collections with bees as one of their specializations. The authors had frequently observed these bees flying low over the ground but had been unable to observe what they were doing. It was only in October 2005, when the authors were sampling flower visitors on the banks of the lagoon at Lamberts Bay (Fig. 13) that the second author noticed a *Serapista rufipes* bee disappearing into the ground. On closer examination it was found that it had entered a plant down tube projecting from the ground. Excavation showed that it had constructed a five-celled, down nest within a, presumably pre-existing, burrow in the sandy soil (Fig. 14). The total length of this nest was 90 mm of which 42 mm was of an entrance tube, 10 mm in diameter. The lower part of the nest containing the cells was 20 mm across at its widest point, at which two cells had been constructed side by side. One cell, from which no emergence had taken place, was opened in June 2006. In it was uneaten provision. Some of this, examined microscopically, was found to contain pollen of mixed provenance, two pollen types being present. Most of the pollen in the sample was spherical and thin-smooth-walled. It was possible that it was from *Conicosia* sp. (Aizoaceae: Mesembryanthema), several large plants of which were growing in close proximity to the nest. A small percentage of the pollen grains, also relatively thin, smooth-walled, were about twice the size, elongate-oval and considerably longer than broad.

In late summer two adults emerged, each making its way out through the side of its cell (Fig. 15).



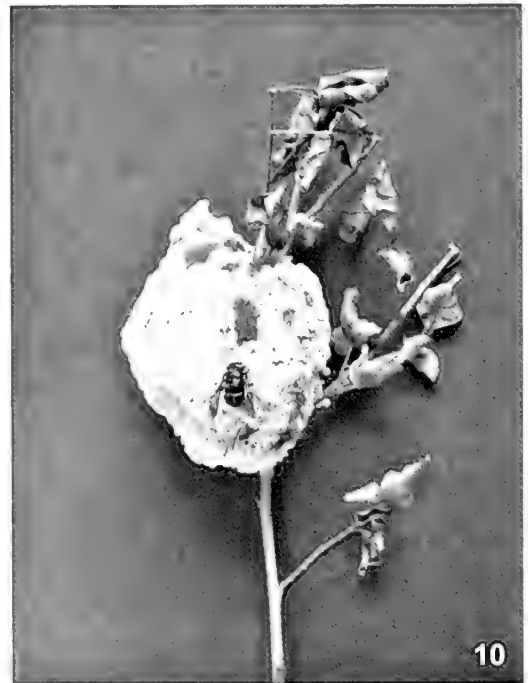


Fig. 8. Strowan Farm, northwest of Grahamstown, Eastern Cape, the area in which nests of *Serapista denticulata* Smith were collected.

Fig. 9. Nest of *Serapista denticulata* Smith constructed on a shrub, *Elytropappus rhinocerotis* (Asteraceae), at Strowan Farm.

Fig. 10. Nest of *Serapista denticulata* Smith constructed on a shrub, *Rhus* sp. (Anacardiaceae) at Goodwin's Kloof, neighbouring Strowan Farm.



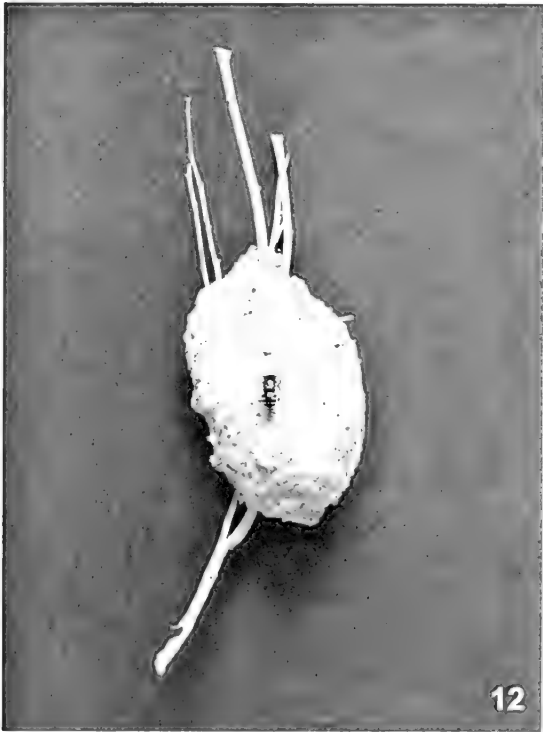


Fig. 11. Southern Kalahari, near Twee Rivieren, Northern Cape, the area in which a nest of *Serapista rufipes* Friese constructed on a shrub, *Lebeckia linearifolia* (Fabaceae: Papilionoideae), as seen in the foreground, was collected.

Fig. 12. Nest of *Serapista rufipes* Friese constructed on a stem of a shrub, *Lebeckia linearifolia* (Fabaceae: Papilionoideae), in the southern Kalahari near Twee Rivieren.



Fig. 13. Southern bank of the lagoon at Lamberts Bay, Western Cape, the area in which a nest of *Serapista rufipes* Friese constructed in a cavity in the ground was found. The clip board on the ground is midway between the site of the nest and a large plant of *Comicosia* (Aizoaceae) beyond the nest.

Fig. 14. Sand cleared away to show nest of *Serapista rufipes* at Lamberts Bay.

Fig. 15. Nest of *Serapista rufipes* Friese from Lamberts Bay showing emergence holes and an imago.

Clearly, *S. rufipes* is remarkable in that it may either construct an aerial nest or may construct its nest within a pre-existing cavity in the ground. The fact that the authors have on several occasions and at several sites observed bees of this species flying low over the ground suggests that the latter strategy may not be unusual.

### *Afranthidium* Michener

The genus *Afranthidium*, divided into eleven sub-genera, is principally sub-Saharan with one sub-genus in the Palaearctic and at least two other species occurring in this region (Michener 2000).

A nest of *A. (Nigranthidium) concolor* (Friese) was found in a bare sandy area on a slope at SorsSors in the Kamiesberg, Namaqualand. It was in an early stage of construction. Projecting from the mouth of a vertical burrow, 6 mm in diameter and 41 mm deep, apparently pre-existing, was a short entrance tube constructed from plant fluff and at the base of the burrow was an open, as yet un-provisioned cell, similarly constructed from plant fluff. Examination of the fluff showed it to have been obtained from the seeds of *Eriocephalus* (Asteraceae) growing nearby.

*Afranthidium (Afranthidium) ablusum* (Cockerell) was found nesting and sheltering (females and males) in empty shells of desert snails, *Trigonephrus* (Mollusca: Gastropoda: Dorcasiidae), in sparsely vegetated, desertic areas north and south of the Orange River, east of Oranjemund and Alexander Bay (Gess and Gess 1999). The cells were embedded in a mass of white, closely packed, cotton-wool like plant fibres. Further nests in *Trigonephrus* shells were found at eight additional sites by the present authors during the course of more extensive sampling and investigation of desert snail shells in 2002, 2003 and 2005. One site, the most southerly, was east of Port Nolloth, Namaqualand, and the other seven were in the Sperrgebiet, Diamond Area no. 1, in the winter rainfall area of Namibia, in the south from the plains in

the vicinity of the Obib Mountains and Boegoeberg northwards to the Klinghardt Mountains and the north/south road west of Grillental.

All the recorded nests of *A. (Immanthidium) junodi* were constructed in pre-existing tubular cavities, which necessitated the construction of the cells in a single linear series, one female nest builder per cavity. Similar nests have been obtained by the present authors from the vicinity of Grahamstown, Eastern Cape. By contrast the nests of *A. (I.) repetitum* are constructed in relatively large cavities. The record published by Michener (1968) is based on part (estimated at one fifth) of a nest removed from an electricity meter box in Estcourt Natal and housed in the Natal Museum. This part of the nest, constructed from plant down, contained an estimated 350 cells or cocoons resulting in the estimation of the total number of cells in the nest having been 1,750 and the conclusion that the nest had been constructed by a considerable group of females.

The remains of a much smaller nest and an associated adult bee of *A. (I.) repetitum* were submitted to the second author for identification. They came from a Cape Town householder who had noticed a bee entering a heavy-duty vice on a workbench in his garage. He had later extracted this nest from a cavity in the vice, in which it had been constructed, and a single cell from an electrical double adapter in the same garage. Regrettably the remains of the nests received were so mangled that no further information could be derived from them. Clearly, the size of the cavity used for nesting will dictate the number of bees which can nest in the cavity and the number of cells which can be constructed.

Subsequently, in June 2000, J. Cardale of CSIRO, Canberra, Australia wrote that this bee had become established in southern Queensland, Australia. Being a nester in pre-existing cavities, the species is an ideal stowaway candidate, making its accidental

transfer with household goods an easy matter.

The origin of the "wool" used by *A. (L.) repetitum* has not been established, however, Taylor (1962) recorded that Jacot Guillarmod had seen *A. (L.) junodi* removing fibres from the stems of *Helichrysum* (Asteraceae) in Lesotho (as Basutoland).

### *Euaspis* Gerstaecker

*Euaspis* is widespread in Africa, from Nigeria to Kenya and south to South Africa, and in southern and eastern Asia (Michener 2000). Of the 12 described species two only are African. *Euaspis* has been recorded as parasitizing other Megachilidae (*Lithurge* and chalicodomiform *Megachile*) (Michener 2000). Iwata (1976: page 420) states of "*Parevaspis* = *Euaspis*" that, "while it is reported to parasitize *Lithurge* (Lieftinck, 1939), observations show that the Japanese *P. basalis* is a cleptoparasite of *Chalicodoma sculpturalis* only (Iwata, 1933). This species does not parasitize any species other than those which make nests with resin. In Southeast Asia, it is reported to live in the nest of *Ch. disjuncta* or other allied species and even in Japan, it probably lives on *Ch. disjunctiformis*". He goes on to give a detailed account of the activities of this bee in converting its host's nest to its own.

Three *Euaspis abdominalis* (Fabricius) were reared from nests of *Megachile (Gronocerus) felina* Gerstaecker from northern Natal by A.J.S. Weaving in 1992 (specimens in the Albany Museum collection). Of these one, a male, is from a nest constructed in an old *Synagris* (Eumeninae) mud nest from Umlalazi Nature Reserve and two, a female and a male, are from a nest constructed within a length of reed put out as a trap-nest in the Lake St Lucia Game Reserve.

Some further support for a possible predilection for parasitising chalicodomiform *Megachile* is given by two observations in the vicinity of Grahamstown. A female *E. abdominalis* was found by R.W. Gess shel-

tering in an aerial mud-nest, probably of *Megachile (Gronocerus) cincta* (Fabricius), build under the windowsill of a brick building (specimen in collection of the Albany Museum). The same was observed investigating holes in a vertical sandstone bank but it was not established which nests were being parasitized although circumstantial evidence suggested that it may have been associated with the nests of *Megachile (Pseudomegachile) schulthessi* Friese (as *Chalicodoma (Pseudomegachile) schulthessi* (Friese)) (Gess 1981).

### DISCUSSION

The discovery that *Serapista rufipes* constructs nests in two very different situations, one exposed above ground and the other within a burrow in the ground, was a surprise. However, nesting by a single species both aerially and in cavities is not unknown in the aculeate hymenoptera, *Celonites michaelsoni* von Schulthess (Vespidae: Masarinae), the cells of which are known to be constructed attached to rocks, albeit in a somewhat sheltered position (as *Celonites gariepensis* Gess – Gess et al 1997), has been found to nest also in pre-existing cavities in the ground (Gess and Gess fieldnotes 1998).

As noted above *Serapista rufipes* has frequently been seen flying low over the ground, suggesting that nesting in the ground may be common. It therefore seems possible that other species of anthidiines which have been found nesting in exposed aerial situations may be found also to nest in cavities, perhaps explaining why so few anthidiine nests have been found.

The construction of spouted pot-shaped resin cells here recorded for *P. (S.) volkmanni* is not unique to *Plesianthidium*. A commonly known example is the European species *Anthidiellum (Anthidiellum) strigatum* Panzer for which there are several published accounts. An account of cell construction, provisioning and closure together with excellent photographic illustrations is to be found in Bellmann (1995,

pages 275–277). Two other examples of spouted pot-shaped resin cells of species of *Anthidiellum* (*Anthidiellum*), *A. notatum* Latreille and *A. perplexum* (Smith), are illustrated by Baker et al. (1985, page 293). The recorded positioning of the cells of *A. (A.) strigatum* and *A. (A.) notatum* differs from that here recorded for *P. (S.) volkmanni*. Instead of being concealed within a cavity they are built in the open. Those of *A. (A.) strigatum* are attached to the sunnyside of tree trunks, plant stems, stones or rocks. The cells of *A. perplexum* illustrated in Baker et al. had been constructed in cavities but, unlike those of *P. (S.) volkmanni*, had been seated in pebbles and separated from each other by cell partitions. Clearly these cells will always be found to be constructed within cavities, however, it should not be assumed that the free-standing cells of *P. (S.) volkmanni* are always constructed within cavities. The fact that *S. rufipes* constructs its nests either on plant stems or in cavities indicates that such an assumption would not be justified. A second but probably constant difference is the orientation of the cells. Whereas the cells of *P. (S.) volkmanni* were all positioned with their long axis sub-horizontal those of *A. (A.) strigatum* and those of *A. notatum* hang down from the substrate so that the ventilation tube points downwards. Closure of the cell is undertaken in a similar manner. Both *P. (S.) volkmanni* and *A. (A.) strigatum*, using their mandibles, crimp the cell wall at the opening in such a way that the edges are drawn inwards leaving only a narrow collar-like opening, much in the way in which a potter draws in the walls of a jug to form the neck. The crimping is not, however, smoothed away but is visible in the completed cells. The spout or ventilation tube is then constructed. Those of *A. (A.) strigatum* and *A. notatum* are slightly flared at the opening whereas that of *P. (S.) volkmanni* is not. Whereas the resin walls of the concealed cells of *P. (S.) volkmanni* are smooth and in colour contrast with the walls of the cavity those of *A. (A.) strigatum*

are camouflaged by the addition of bark fragments to the resin giving the outer surface a flaky finish which furthermore in colour blends with that of the substrate.

## FLOWER VISITING

In a study of host plant specialization in western Palaearctic anthidiine bees (Muller 1996), pollen sources of 72 anthidiine species of Europe, North Africa and Asia Minor were investigated by analysis of pollen loads from females. Muller found that 43% of the species studied by him were oligolectic (relatively specialized as to pollen source), 35% were polylectic (visiting up to 17 plant families for pollen), and the remaining 4% insufficiently known. The principal pollen sources throughout were Fabaceae, Lamiaceae, Asteraceae, Dipsacaceae, Campanulaceae, and Zygophyllaceae. Of these all except Dipsacaceae are families included in the list of families visited by southern African anthidiines.

In the comparative overview of flower visiting by non-*Apis* bees in the semi-arid to arid areas of southern Africa (Gess and Gess 2004) the Gesses reported that of the 34 plant families found to be attracting visits to flowers by bees 30 were visited by Megachilidae (Gess and Gess 2004: Table 2) and of these 20 were visited by anthidiines (Gess and Gess 2004: Table 5). Of the plant families Fabaceae (almost exclusively Papilionoideae) received visits from 61% of the 44 species of anthidiines for which records were obtained. The three other families receiving visits from a significant, though appreciably lower, percentage of the species of anthidiines are Asteraceae (32%), Malvaceae (all species of *Hermannia*, formerly Sterculiaceae) (27%) and Lamiaceae (23%).

In the overview (Gess and Gess 2004) flower visiting within the Megachilidae was compared between sub-families and tribes. Values for Diversity of Choice (see Methods, present paper) were calculated at the family level. The values obtained were – Andrenidae 177.77, Apidae 195.93, Col-

Table 1. Numbers of species by genus of Anthidiini (Megachilinae) recorded visiting flowers of the listed plant families. Numbers of species below generic names denote the number of species for which flower visiting records are available. Numbers before asterisks denote the numbers of species for which five or more such records were obtained.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
<i>Afranthidium</i>			5	2	1	2	13			5		2	1	1		3		1	6	1
21 species			1*			1*	6*			2*			1*						2*	
<i>Anthidiellum</i>										1		2								
1 species																				
<i>Anthidioma</i>							1													
1 species																				
<i>Anthidium</i>							1								1	1			1	
3 species																				
<i>Aspidosmia</i>				1			1												1	
2 species							1*												1*	
<i>Cyphanthidium</i>							1					1			1					
2 species															1*					
<i>Eoanthidium</i>							1		1			1			1					
1 species							1*					1*			1*					
<i>Pachyanthidium</i>				1		1	3				1	1							1	
3 species						1*	3*													
<i>Plesianthidium</i>	1	1	4			1	5	2	1	5		2			1	5			2	
6 species						1*	3*			1*		1*			1*					
<i>Pseudoanthidium</i>															1	1			2	
2 species																1*			1*	
<i>Serapista</i>							1			1				1				1	2	
2 species							1*			1*										
<i>Trachusa</i>							1													
1 species							1*													
Total number of species (45)	1	1	9	4	1	4	28	2	2	12	1	9	1	2	5	10	2	1	15	1
		1*	1*			3*	16*			4*		2*	1*	3*	3*	1*			8*	

A = Asphodelaceae; B = Iridaceae; C = Aizoaceae; D = Amaranthaceae; E = Molluginaceae; F = Zygophyllaceae; G = Fabaceae; H = Polygalaceae; I = Brassicaceae; J = Malvaceae; K = Loasaceae; L = Boraginaceae; M = Vahliaceae; N = Apocynaceae; O = Acanthaceae; P = Lamiaceae; Q = Scrophulariaceae; R = Apiaceae; S = Asteraceae; T = Campanulaceae.

letidae 50.00, Halictidae 202.90, Megachilidae 130.61, Melittidae 70.00. When the formula is applied to Table 1 a value of 146.67 is obtained for Anthidiini. This suggests a relatively high degree of polyphagy for the Anthidiini overall. However, whereas some of the solitary apids were recorded from flowers of over twenty families no anthidiine was recorded from more than seven families.

In the present contribution flower visiting at the levels of genera and for some genera sub-genera and species are examined. In most cases the number of females is too low for analysis of their pollen loads to give an accurate evaluation of oligolecty

and polylecty and so this has not been attempted. However, summation of flower visiting records for females and males does give some indication of preferences for and differences in preferences for flowers of particular taxa and possibly degree of oligophagy and polyphagy (diversity of plants visited to obtain pollen and nectar combined) within the southern African anthidiines.

At the generic level nine of the 13 genera of anthidiines included were recorded from Fabaceae, however, none was restricted to Fabaceae, flowers of 1–13 plant families being visited. However, if numbers of records of visits to Fabaceae

Table 2. Numbers of species by subgenus of *Afranthidium* (Megachilinae: Anthidiini) recorded visiting flowers of the listed plant families. Numbers of species following generic names denote the number of species for which flower visiting records are available. Asterisks denote the numbers of species for which five or more such records were obtained.

	Afranth-5 spp.	Branth-6 spp.	Capanth-1 sp.	Domanth-1 sp.	Immanth-3 spp.	Nigranth-1 sp.	Oranth-3 spp.
Aizoaceae	2	2*				1	
Molluginaceae							1
Amaranthaceae		2					
Zygophyllaceae	1	1					
Fabaceae	5**	4****			1*		3
Malvaceae	1	1		1			2**
Boraginaceae					2		
Vahliaceae		1					
Apocynaceae		1			3		
Lamiaceae					1		
Scrophulariaceae					1		
Asteraceae		2*	1*		1	1	
Campanulaceae		2					

compared with visits to other plant families are considered (Table 1), Fabaceae is the most frequently visited family.

When visiting is considered at sub-generic and specific levels, some possible differences in preferences are apparent. Of the seven sub-genera of *Afranthidium* (Table 2), only four were recorded from Fabaceae. Of these, two of the five species of *A. (Afranthidium)*, four of the six species of *A. (Branthidium)* and one of the three species of *A. (Immanthidium)* were recorded five or more times from Fabaceae but none of the three species of *A. (Oranthidium)* was recorded five or more times. Two species of *Oranthidium* were, however, the only species of the genus *Afranthidium* recorded five or more times from *Hermannia* (Malvaceae). One species of *A. (Branthidium)* and the single species of *A. (Capanthidium)* (not recorded from flowers of any other plant family) were recorded at least five times from Asteraceae.

When flower visiting records for the six species of *A. (Branthidium)* are separated (Table 3), it is seen that *braunsi*, *haplogastrum*, *matjiesfonteinense* and *minutulum* were recorded 29 (14 female and 15 male), 11 (seven female and four male), 7 (one female and six male) and 17 (12 female and five male) times respectively from Fabaceae suggesting a preference for Fabaceae

by at least three of these species. However, *minutulum* was recorded 30 (15 female and 15 male) times from Asteraceae suggesting an equal, if not greater, preference for Asteraceae. This species was furthermore recorded seven times (five female and two male) from Aizoaceae and was also found visiting flowers of four other families suggesting that this species at least is polyphagous.

Of the three sub-genera of *Plesianthidium* (Table 4) all were recorded from Fabaceae and furthermore the single species of *P. (Carinanthidium)*, the single species of *P. (Spinanthidiellum)* and two of the four species of *P. (Spinanthidium)* were recorded five or more times from Fabaceae. In addition, one of the four species of *P. (Spinanthidium)* was recorded five or more times from Boraginaceae and one five or more times from Malvaceae (*Hermannia* only).

When the flower visiting records for the four species of *P. (Spinanthidium)* are separated (Table 5), it is seen that *neli* and *trachusiforme* were recorded from Fabaceae 18 (5 female and 13) and 19 (6 female and 13 male) times respectively suggesting a possible preference by these species for Fabaceae. The records of three female and



Table 3. Numbers of records by species of the subgenus *Branthidium* of the genus *Afranthidium* (Megachilinae: Anthidiini) of visits to flowers of the listed plant families.

	<i>braunsi</i>	<i>guillarmodi</i>	<i>haplogastrum</i>	<i>? jocosum</i>	<i>matjiesfonteinense</i>	<i>minutulum</i>
Aizoaceae			2			7
Amaranthaceae	2		2			
Zygophyllaceae						3
Fabaceae	29		11		7	17
Malvaceae						2
Vahliaceae						4
Apocynaceae						1
Asteraceae	3					30
Campanulaceae		1		1		

two male of *tachusiforme* from Boraginaceae probably indicate a possible secondary preference only. The species for which more than five records were obtained from Malvaceae is *callescens* (5 female and 12 male). Although this may possibly indicate a preference it should be noted that only five of the 17 records are for females and that two females were recorded from Lamiaceae and one female from Asteraceae.

Further sampling of flowers for anthidiines would clearly be rewarding and would make more substantiated conclusions with respect to flower preferences possible.

Table 4. Numbers of species by subgenus of *Plesianthidium* (Megachilinae: Anthidiini) recorded visiting flowers of the listed plant families. Asterisks denote the numbers of species for which five or more such records were obtained.

	<i>Carinanthidium</i> 1 species	<i>Spinanthidiumellum</i> 1 species	<i>Spinanthidium</i> 4 species
Asphodelaceae	1		
Iridaceae			1
Aizoaceae		1	3
Zygophyllaceae	1	1	
Fabaceae	1*	1*	3**
Polygalaceae	1	1	
Brassicaceae			1
Malvaceae		1	4*
Boraginaceae			1*
Acanthaceae			
Lamiaceae	1	1	3*
Asteraceae	1		1

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Table 5. Numbers of records by species of the subgenus *Spinanthidium* of the genus *Plesianthidium* (Megachilinae: Anthidiini) of visits to flowers of the listed plant families.

	<i>bruniceps</i>	<i>callescens</i>	<i>neli</i>	<i>trachusiforme</i>
Iridaceae			1	
Aizoaceae	1		2	2
Fabaceae	3		18	19
Brassicaceae				
Malvaceae	1	17	3	1
Boraginaceae			1	5
Lamiaceae	2	6		2
Asteraceae		2		

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APPENDIX: FLOWER VISITING  
RECORDS FOR ANTHIDIINE BEES  
(HYMENOPTERA: MEGACHILIDAE:  
MEGACHILINAE: ANTHIDIINI) IN  
SOUTHERN AFRICA

The data given below, except where indicated, are condensed from the authors' collection labels. Many of the specimens were collected after the catalogue (Gess and Gess, 2003) and the electronic bee database were closed in March 2002. Full locality data, including co-ordinates, and exact dates of all specimens are available from label data and of those for specimens processed before March 2002 are available from the electronic, relational database.

*Afranthidium* Michener – eleven sub-genera, 10 found in the Afrotropical Region (Michener 2000).

*Afranthidium (Afranthidium)* Michener – known from the “Cape Province”, South Africa, and from Namibia (Michener 2000). Pasteels (1984) includes nine species but Michener (2000) considers that some may belong elsewhere.

*Afranthidium (A.) ablusum* (Cockerell): Fabaceae (Papilionoideae), *Aspalathus*, 3♂♂, Clanwilliam in the Olifants River Valley in the Western Cape, early October.

*Afranthidium (A.) biangulatum* Pasteels: Fabaceae (Papilionoideae), *Indigofera*, 2♀♀, between Rosh Pinah and Sendelingsdrif, Namibia, mid-October; Aizoaceae (Mesembryanthema), 1♀, between Steinkopf and Vioolsdrif in northern Namaqualand, mid-October.

*Afranthidium (A.) hamaticauda* Pasteels: Fabaceae (Papilionoideae), *Indigofera* and *Lebeckia*, 11♀♀ and 11♂♂, six sites from Wallekraal, Northern Cape to Lüderitz, Namibia, late September to early October; Malvaceae (formerly Sterculiaceae), *Hermannia*, 1♂, Wallekraal and 14♀♀, northeast of Aus and at Swakopmund in Namibia, early to mid-September; Zygophyllaceae, *Zygophyllum*, 6♀♀ and 11♂♂, Swakopmund, Namibia, mid-March.

*Afranthidium (A.) karoense* (Brauns): Fabaceae (Papilionoideae), *Indigofera*, 4♀♀ and 5♂♂, in the vicinity of Oranjemund and Aus, Nami-

bia, late September and early March; Aizoaceae (Mesembryanthema), 2♀♀ and 1♂, Richtersveld and southeastern Namaqualand, Northern Cape, late September; Zygophyllaceae, 2♀♀ and 1♂, Richtersveld and southeastern Namaqualand, Northern Cape, late September.

*Afranthidium (A.) reicherti* Brauns: Fabaceae (Papilionoideae), *Aspalathus* and *Psoralea*, 1♀ and 2♂♂, vicinity of Ceres and of Oudtshoorn, Western Cape, late October and early December.

*Afranthidium (Branthidium)* Pasteels – found from Lesotho to the Western Cape, north to Zaire and Kenya (Michener 2000). Pasteels (1984) recognized 10 species.

*Afranthidium (B.) braunsi* (Fries): Fabaceae (Papilionoideae), *Aspalathus* and *Indigofera*, 15♀♀ and 19♂♂, southwestern Cape, mid-October and late-November, and south and north of the Orange River, western Northern Cape and southwestern Namibia, late-September to mid-October; Amaranthaceae, *Hermibstaedtia*, 2♂♂, Richtersveld, Northern Cape, late-September; Asteraceae, *Tripteris*, 2♀♀, 1♂, north of the Orange River, western Northern Cape, mid-October.

*Afranthidium (B.) guillarmodi* (Mavromoustakis): Campanulaceae, *Wahlenbergia*, 1♀, northwest of Grahamstown, Eastern Cape, early-March.

*Afranthidium (B.) haplogastrum* (Mavromoustakis): Fabaceae (Papilionoideae), *Indigofera* and *Lessertia*, 12♀♀ and 6♂♂, three localities in Namaqualand and from Aus, Namibia, early-September to mid-October; Aizoaceae (Mesembryanthema), *Prenia*, 2♀♀, Springbok, Namaqualand, early October; Amaranthaceae, *Hermibstaedtia*, 1♀ and 1♂, Richtersveld, late-September.

*Afranthidium (B.) ? jocosum* Pasteels: Campanulaceae, *Wahlenbergia*, 1♂, between Okahandja and Karibib, northwestern Namibia, late-March.

*Afranthidium (B.) matjesfonteinense* (Mavromoustakis): Fabaceae (Papilionoideae), *Indigofera*, 1♀ and 6♂♂, Richtersveld, Northern Cape, late-September.

*Afranthidium (B.) minutulum* (Brauns): Fabaceae (Papilionoideae), mainly *Indigofera*, 6♀♀ and 11♂♂, six sites from the Orange River north to Omaruru in northwestern Namibia, late-February to early-April; Aizoaceae (Mesembryanthema), 5♀♀ and 2♂♂, Augrabies on the

Orange River north to Karibib in northwestern Namibia, late-February, mid-April, mid-October; Asteraceae, *Geigeria* and *Osteospermum* (including *Tripteris*), 17♀♀ and 16♂♂, Orange River north to Usakos in northwestern Namibia, mid-March and mid-October; Aizoaceae (non-Mesembryanthema), 5♀♀, 2♂♂, Augrabies, Orange River, Northern Cape, northwestern Namibia, late-February to early-April; Apocynaceae, *Asclepias*, 1♂, southeastern Namibia, mid-March; Malvaceae, *Hermannia*, 1♀, 1♂, Gibeon, southern Namibia, Büllsport, western central Namibia, late-March, mid-April; Vahliaceae, *Vahlia*, 3♀, 1♂, southeastern Namibia, early-March; Zygophyllaceae, *Zygophyllum*, 2♀, 1♂, Richtersveld and northwestern Namibia, early-October, late March to early April.

***Afranthidium (Capanthidium)*** Pasteels - has a disjunct distribution, southern Africa (Cape Province, South Africa and Namibia) and western Mediterranean (Morocco and Spain) (Michener 2000). Ten species were recognized from southern Africa by Pasteels (1984). There appear to be no records of nesting for this sub-genus.

***Afranthidium (C.) capicola*** (Brauns): Asteraceae, 11♀♀, 8♂♂, Oudtshoorn in the Little Karoo and Karoo Poort near Ceres, Clanwilliam and between Clanwilliam and Klawer in the Olifants River Valley, early December, late October.

***Afranthidium (Domanthidium)*** Pasteels, monospecific, found in Namibia and South Africa, in the "Cape Province", probably also Natal (Michener 2000).

***Afranthidium (D.) abdominale***: Malvaceae (formerly Sterculiaceae), *Hermannia*, 1♂ between Murraysberg and Hutchinson, central Nama Karoo, South Africa, late-October.

***Afranthidium (Immanthidium)*** Pasteels is widespread in eastern Africa from Sudan to South Africa, Natal west to "Cape Province", and Namibia (Michener 2000).

***Afranthidium (I.) immaculatum*** (Smith): Asteraceae, *Senecio*, 1 specimen, Bastervetpad [near Barkly East], Eastern Cape, South Africa; Scrophulariaceae, *Diascia capsularis* and *Diascia fetacaniensis*, 2 specimens, Mt Kemp and Zuurborg Pass, Eastern Cape (col. V.B.Whitehead, det. C.D.Michener, specimens in South African Museum, Cape Town)

***Afranthidium (I.) junodi*** (Fries): Fabaceae (Papilionoideae), *Melolobium*, *Aspalathus* and "lu-

cerne", 4♀♀, 1♂♂, northeast Grahamstown, Eastern Cape, Clanwilliam, Olifants River Valley, Western Cape, Augrabies, Orange River, Northern Cape, late September, mid-October, late February; Lamiaceae, *Ballota*, 2♀♀, Kamiesberg, Namaqualand, Northern Cape, early-October; Asteraceae, *Berkheya*, 1♀, Eastern Cape, late-September; Boraginaceae, *Trichodesma*, 1♀, Richtersveld, Northern Cape, late-September.

***Afranthidium (I.) repetitum*** (Schulz): Lamiaceae, 1♂, Richtersveld, Northern Cape, late-September.

***Afranthidium (I.) sjoestedti*** (Fries): Lamiaceae, *Ballota*, 3♂♂, southeastern Namaqualand and Richtersveld, Northern Cape, late-September; Boraginaceae, *Anchusa*, 1♂, Grahamstown, Eastern Cape, late September.

***Afranthidium (Nigranthidium)*** Pasteels - found in Namibia and in "Cape Province", South Africa (Michener 2000). There are two named species and a third undescribed species (Michener 2000).

***Afranthidium (Nigranthidium) concolor*** (Fries): Aizoaceae (Mesembryanthema), *Herrea*, 2♀♀, Nieuwoudtville, southeastern Namaqualand, late-September; Asteraceae, *Pentzia*, *Senecio*, 3♀♀, southeastern Namaqualand, northern Namaqualand, Northern Cape, September.

***Afranthidium (Oranthidium)*** Pasteels - represented by five or six species, has been found in Namibia and in South Africa, "Cape Province" east to the "Transvaal" (Michener 2000).

***Afranthidium (O.) folliculosum*** (Buysson): Fabaceae (Papilionoideae), *Indigofera*, 1♀, Kalahari fringe, southeastern Namibia, late-March.

***Afranthidium (O.)* sp. Gess 1**: Fabaceae (Papilionoideae), *Indigofera*, 3♀♀, Kalahari fringe, southeastern Namibia, late March; Malvaceae, *Hermannia*, 4♀♀ and 11♂♂, Kalahari fringe, southeastern Namibia, Northern Cape, early-March, early-April; Apiaceae, *Deverra*, 1♀, 1♂, southern Kalahari, early-March; Molluginaceae, *Limeum*, 2♀♀, southern Kalahari, Northern Cape, early March.

***Afranthidium (O.)* sp. Gess 2**: Fabaceae (Papilionoideae), *Indigofera*, 1♂, east of Oranjemund, northern bank of the Orange River, southwestern Namibia, late-September; Malvaceae, *Hermannia*, 8♀♀, Springbok and Kamiesberg, Namaqualand, Northern Cape, late September, early-October.

- Anthidiellum** Cockerell - five sub-genera are recognized (Michener 2000). Of these only two, *Chloranthidiellum* Mavromoustakis and *Pycnanthidiellum* Krombein, have been recorded from Africa south of the Sahara.
- Anthidiellum* near *melanocephalum* (syn. of *apicatum* Smith): Euphorbiaceae, *Dalechampia volubilis* E. Mey. ex Baill., False Bay, northern KwaZulu-Natal (Armbruster and Steiner 1992).
- Anthidiellum* (*Pycnanthidiellum*) *spilotum* (Cockerell): Malvaceae (formerly Tiliaceae), *Grewia occidentalis* L., 1♂, northeast of Grahamstown, Eastern Cape, early December.
- Anthidioma** Pasteels - known from Namibia and the Western Cape, South Africa from two species, one undescribed (Michener 2000).
- Anthidioma* sp.: Fabaceae (Papilionoideae), "yellow legume", one specimen, from Pomona, Sperrgebiet, southwestern Namibia (col. V. Whitehead, det. C.D. Michener, specimen in South African Museum, Cape Town.)
- Anthidium** Michener - found on all continents except Australia; rather poorly represented in sub-Saharan Africa (Michener 2000).
- Anthidium** (*Anthidium*) Fabricius - found throughout the range of the genus; represented in Africa by only a few species (Michener 2000).
- Anthidium* (*A.*) *pontis* (Cockerell): Acanthaceae, *Blepharis capensis* (L. f.) Pers., 1♀, northeast Grahamstown, Eastern Cape, early January.
- Anthidium** (*Nivanthidium*) Pasteels - known from only one species; apparently previously recorded only from eastern Africa (Mozambique and Malawi) (Michener 2000).
- Anthidium* (*N.*) *niveocinctum* Gerstaecker: Asteraceae, *Geigeria*, 2 ♀♀, Oshivelo, Namibia, early-April (D.W. & G.T. Gess).
- Anthidium** (*Severanthidium*) Pasteels - known from the Eastern Cape north to Senegal and the Arabian Peninsula (Michener 2000).
- Anthidium* (*Severanthidium*) *soni* Mavromoustakis: Fabaceae (Papilionoideae), *Crotalaria*, 1♂, Kamanjab, Namibia, late-March.
- Aspidosmia** Brauns, represented by two species only - known solely from Namibia and the "Cape Province" (Michener 2000).
- Aspidosmia* *arnoldi* (Brauns): Fabaceae (Papilionoideae), *Lebeckia* and *Wiborgia*, 3♀♀, 3♂♂, four sites from Clanwilliam to Springbok, early-late-September; Lamiaceae, *Stachys*, 1♀, Richtersveld, Northern Cape, late September.
- Aspidosmia* *volkmanni* (Fries): Asteraceae, *Berkheya*, *Gorteria* and *Osteospermum*, 18♀♀, 33♂♂, four sites from Kamiesberg to north of the Orange River, late-September, early-October; Amaranthaceae, *Hermibstaedia*, 2♀♀, Richtersveld, Northern Cape, late-September.
- Cyphanthidium* Pasteels - known from Zimbabwe, Namibia and the "Cape Province" from three species, two described (Michener 2000).
- Cyphanthidium* *intermedium* Pasteels: Fabaceae (Papilionoideae), *Crotalaria* and *Indigofera*, 1♀, 2♂♂, three sites in western Namibia, Rosh Pinah/Sendelingsdrif (south), Uis/Henties Bay and Khorixas (north), mid-October (south), early April (north).
- Cyphanthidium* sp.: Acanthaceae, *Blepharis*, 3♀♀, 3♂♂, between Springbok and Kamieskroon in Namaqualand, October.
- Euanthidium** Popov - known from Africa, the Middle East, the Indian Peninsula and Asia (Michener 2000); divided into four sub-genera, two of which, *Clistanthidium* Michener and *Griswold* and *Euanthidium* Popov are represented in Africa south of the Sahara but only the former from southern Africa (Michener 2000).
- Euanthidium*. (*Clistanthidium*) *turnericum* (Mavromoustakis): Fabaceae (Papilionoideae), *Indigofera*, "a yellow flowered papilionate shrub", 1♀, 2♂♂, Richtersveld, Northern Cape, between Rosh Pinah and Sendelingsdrif, southwestern Namibia, late-September, mid-October; Acanthaceae, *Monechma* and *Petalidium*, 6♂♂, Richtersveld, Northern Cape, between Uis and Henties Bay, northwestern Namibia, late-September (south), early-April (north); Boraginaceae, *Heliotropium*, 1♀, between Uis and Omaruru, northwestern Namibia, March; Boraginaceae (formerly Hydrophyllaceae), *Codon*, 3♀♀, 3♂♂, Richtersveld, Northern Cape, between Uis and Henties Bay, northwestern Namibia, late September (south), early April (north); Brassicaceae (formerly Capparaceae), *Cleome*, 1♀, 1♂, between Bullsport and Sesriem, westcentral Namibia, mid-April.
- Pachyanthidium** Fries - known from Africa east to China (Michener 2000); four sub-genera recognized; all present in Africa south of the Sahara; only three recorded from southern Africa (Michener 2000).
- Pachyanthidium** (*Ausanthidium*) Pasteels, known from a single species found in Namibia.

*Pachyanthidium* (A.) *ausense* (Mavromoustakis): Fabaceae (Papilionoideae), *Indigofera*, 1♀, 8♂♂, east of Oranjemund, southwestern Namibia, east of Alexander Bay, Richtersveld, Northern Cape, late September; Amaranthaceae, *Hermibstaedtia*, 2♂♂, Richtersveld, late September; Boraginaceae, *Trichodesmia*, 2♂♂, Richtersveld, late September; Zygophyllaceae, *Zygophyllum*, 2♀♀, 5♂♂, Richtersveld, between Palm and Khorixas in northwestern Namibia, late-September (south), early-April (north); Loasaceae, *Kissenia*, 3♂♂, between Keetmanshoop and Aus in southwestern Namibia, between Uis and Henties Bay, northwestern Namibia, early March (south), early April (north); Malvaceae (formerly Sterculiaceae), *Hermannia*, 2♂♂, southwest of Aus, southwestern Namibia, September.

*Pachyanthidium* (*Pachyanthidium*) Friese - widespread in Africa, from Senegal to Ethiopia and south to KwaZulu-Natal and the Cape Province, South Africa; 11 species (Michener 2000).

*Pachyanthidium* (P.) *cordatum* (Smith): Fabaceae (Papilionoideae), *Psoralea pinnata* L., 1♀, near Grahamstown, Eastern Cape (Jacot Guillarmod label data); Euphorbiaceae, *Dalechampia* sp., northern KwaZulu-Natal (Armbruster and Steiner 1992).

*Pachyanthidium* (*Trichanthidium*) Cockerell - known in Africa from the Ivory Coast to southern Egypt, south to Angola and KwaZulu Natal, South Africa, and in Asia from India to Yunnan Province, China; "at least three species" (Michener 2000).

*Pachyanthidium* (T.) *benguelense* (Vachal): Fabaceae (Papilionoideae), *Aspalathus*, 1♀, Graafwater, west of the Olifants River, Western Cape, late September; Asteraceae, *Senecio*, 1♂, near Grahamstown, Eastern Cape, late December.

*Plesianthidium* Cameron, known from South Africa only, principally from the west; consisting of four sub-genera, *Carinanthidium* Pasteels, *Plesianthidium* Cameron, *Spinanthidiellum* Pasteels, and *Spinanthidium* Mavromoustakis (Michener 2000).

*Plesianthidium* (*Carinanthidium*) Pasteels, represented by a single species found in the Western Cape, but the type specimen was reported to be from the "northern Transvaal" (Michener 2000).

*Plesianthidium* (C.) *cariniventre* (Friese): Fabaceae (Papilionoideae), *Aspalathus* and *Lebeckia*, 4♀,

19♂♂, Olifants River Valley, Western Cape, Namaqualand, Northern Cape, late-September, early-October; Polygalaceae, *Polygala*, 1♀, Namaqualand, late-October; Asteraceae, *Pteronia*, 1♀, Namaqualand, early-October; Lamiaceae, *Ballota*, 1♀, Namaqualand, early-October; Zygophyllaceae, *Zygophyllum*, 3♂♂, Namaqualand, early-October; Asphodelaceae, *Albuca*, 1♂, Namaqualand, late September.

*Plesianthidium* (*Spinanthidiellum*) Pasteels - known from two species from the Western Cape Province of South Africa (Michener 2000).

*Plesianthidium* (S.) *volkmanni* (Friese): Fabaceae (Papilionoideae), mostly *Aspalathus* and *Lebeckia*, 34♀♀, 68♂♂, Western Cape, Namaqualand, Northern Cape, early-September to late-October; Malvaceae (formerly Sterculiaceae), *Hermannia*, 1♀, southeastern Namaqualand, late-September; Zygophyllaceae, *Zygophyllum*, 1♀, 4♂♂, southeastern Namaqualand, late-September; Lamiaceae, *Stachys*, 3♂♂, southeastern Namaqualand, late-September; Aizoaceae (Mesembryanthema), *Herrea*, 2♂♂, southeastern Namaqualand, late-September; Polygalaceae, *Polygala*, 2♂♂, Namaqualand, late-September, late-October.

*Plesianthidium* (*Spinanthidium*) Mavromoustakis - known from five species all from the "Cape Province", South Africa (Michener 2000).

*Plesianthidium* (S.) *brunepes* (Friese): Fabaceae (Papilionoideae), *Lebeckia*, 2♀♀, 1♂, Namaqualand, Northern Cape, early-September; Aizoaceae (Mesembryanthema), *Herrea*, 1♀, near Springbok, Namaqualand, early-October; Lamiaceae, *Ballota* and *Stachys*, 3♂♂, near Springbok, early-October; Malvaceae (formerly Sterculiaceae), *Hermannia*, 1♂, Kamiesberg, Namaqualand, early-October.

*Plesianthidium* (S.) *callescens* (Cockerell): Asteraceae, *Arctotheca* and *Pteronia*, 1♀, 1♂, Namaqualand, Northern Cape, late-September; Lamiaceae, *Ballota*, 2♀, 4♂, southeastern Namaqualand, late-September; Malvaceae (formerly Sterculiaceae), *Hermannia*, five species, 2♀♀, 15♂♂, Namaqualand, Ratelfontein, Western Cape, late-September, early-October.

*Plesianthidium* (S.) *neli* (Brauns): Fabaceae (Papilionoideae), *Aspalathus*, *Lebeckia* and *Melolobium*, 5♀, 13♂♂, western Western Cape, Namaqualand, early-September, early-October; Aizoaceae (Mesembryanthema), *Prenia*,

2♂♂, near Ratelfontein, western Western Cape, early-October; Boraginaceae, *Anchusa*, 1♂, Kamiesberg, Namaqualand, early October; Malvaceae (formerly Sterculiaceae), *Hermannia* 1♀, 2♂♂, Namaqualand, late-September, early-October; Iridaceae, *Homeria*, 1♀, vicinity of Springbok, Namaqualand, early-October.

*Plesianthidium* (S.) *trachusiforme* (Fries): Fabaceae (Papilionoideae), *Aspalathus*, *Lebeckia*, *Wiborgia*, *Melolobium* and *Indigofera*, 6♀♀, 13♂♂, Olifants River Valley and westwards, Western Cape, Namaqualand, Northern Cape, early-September to mid-October; Aizoaceae (Mesembryanthema), *Herrea*, 2♀♀, Springbok, Namaqualand, early-September, early-October; Boraginaceae, *Anchusa*, 3♀♀, 2♂♂, Kamiesberg, Namaqualand, early-October; Brassicaceae, *Heliophila*, 1♀, Kamiesberg, early-September; Lamiaceae, *Ballota*, 2♂♂, Kamiesberg, early-October; Malvaceae (formerly Sterculiaceae), *Hermannia*, 1♂, Nieuwoudtville, southeastern Namaqualand, late-September.

*Pseudanthidium* (*Tuberanthidium*) Pasteels, four species are recognized – known from Tanzania, Botswana, Namibia, Lesotho, and South Africa, “Cape Province to Natal” (Michener 2000).

*Pseudanthidium* (T.) *tuberculiferum* (Brauns): Asteraceae, *Berkheya* and *Pteronia*, 5♀♀, 4♂♂, Nieuwoudtville, southeastern Namaqualand, Springbok, Namaqualand, Northern Cape, northwest of Aus, southwestern Namibia, late-September; Acanthaceae, *Monechma*, 1♂, Richtersveld, Northern Cape; Lamiaceae, *Ballota* and “labiate”, 5♂♂, Nieuwoudtville, Kamiesberg, Richtersveld, Namaqualand, early-late-September, Acanthaceae, *Monechma*, 1♂, Richtersveld, Northern Cape, late September.

*Pseudanthidium* (T.) *damarensis* (Mavromoustakis): Asteraceae, *Giegeria*, 1♀, 2♂♂, between Oshivelo and Ondongwa, northern Namibia, early-April (D.W. and G.T. Gess).

*Serapista* Cockerell – known from the Afrotropical Region, two of the four species represented in southern Africa – widespread *S. denticulata* (Smith) recorded from central, eastern and southern Africa and more restricted *S. rufipes* (Fries) recorded only from southern Africa (Pasteels, 1984).

*Serapista rufipes*: Fabaceae (Papilionoideae), *Crotalaria*, *Indigofera*, *Lebeckia* and *Aspalathus*, 21♀♀, 16♂♂, 14 sites in Namibia, Nababeep, Namaqualand, Northern Cape, four sites in Olifants River Valley and vicinity, Western Cape, early-March to early-April (north), mid-October (south); Malvaceae (formerly Sterculiaceae), *Hermannia*, 9♀♀, 6♂♂, six sites in Namibia, two sites in Namaqualand, early-March to late-April (north), early-September to early-October (south); Acanthaceae, *Monechma*, 1♀, northwest Namibia, late-April; Brassicaceae (formerly Capparaceae), *Cleome*, 1♂, northwest Namibia, late-April; Scrophulariaceae, *Jamesbrittenia*, 1♀, westcentral Namibia, mid-April; Apocynaceae, *Asclepias*, 1♀, 1♂, southern Karoo, Western Cape, late-November.

*Trachusa* Panzer – known from Africa, Asia, the Mediterranean and North America. The sub-genus *Massanthidium* Pasteels is known from four species – three described by Pasteels, from Kenya and Eritrea and one recorded from a single specimen from Namibia by Michener (2000). In the course of their survey of flowers visited by aculeate wasps and bees in the semi-arid to arid areas of southern Africa the authors encountered an undescribed species in northwestern Namibia, most probably the species known to Michener from a single specimen. Eighteen females and five males were collected.

*Trachusa* (*Massanthidium*) sp. undescribed: Fabaceae (Papilionoideae), *Crotalaria* and *Indigofera*, 2♀, 2♂, west of Palm in northwestern Namibia, west-northwest of Omatjete in northwestern Namibia, late-March; Fabaceae (Caesalpinoideae), *Adenolobus*, 4♀♀, 1♂, between Palm and Khorixas and a drainage channel between Gaub and Kuiseb passes, northwestern Namibia, mid-late-March; Pedaliaceae, *Sesamum*, 6♀♀, south of Swartbooisdrif, Kunene River, northwestern Namibia, late-March; Brassicaceae (formerly Capparaceae), *Cleome*, south of Swartbooisdrif, late-March; Acanthaceae, *Monechma*, 5♀♀, 1♂, Two Palms, Palmwag, northwestern Namibia, late-March; Lamiaceae, *Hemizygia*, 1♂, south of Palmwag, late-March.



## Diversity, Classification and Higher Relationships of Mymarommatoidea (Hymenoptera)

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**Abstract.**—The supraspecific, extinct and extant fauna of Mymarommatoidea (Hymenoptera) is revised. Ten extinct and ten extant described species are classified in six genera and two families, Mymarommatidae and Gallorommatidae **n. fam.** A key to the families and genera is provided. Classified in Gallorommatidae is the extinct Cretaceous genus, *Galloromma* Schlüter, including the type species, *G. bezonnaisensis* Schlüter, and *G. agapa* (Kozlov and Rasnitsyn) **n. comb.** (from *Palaeomymar*). Classified in Mymarommatidae is one extinct Cretaceous genus, *Archaeomma* Yoshimoto, one extinct Tertiary genus, *Palaeomymar* Meunier, and three extant genera, *Mymaromma* Girault, *Mymaromella* Girault, and *Zealaromma* **n. gen.** *Mymaromma* and *Mymaromella* **rev. stat.** are resurrected from prior synonymy under *Palaeomymar* and a neotype male is designated for *Palaeomymar succini* Meunier. *Protooctonus* Yoshimoto is transferred from Mymaridae to Mymarommatidae and is newly synonymised under *Archaeomma*. Newly classified in *Archaeomma* are the Cretaceous species *A. masneri* (Yoshimoto) **n. comb.** (from *Protooctonus*), and *A. mandibulatum* (Kozlov and Rasnitsyn) **n. comb.**, *A. senonicum* (Kozlov and Rasnitsyn) **n. comb.** and *A. japonicum* (Fursov, Shirota, Nomiya and Yamagishi) **n. comb.** (all from *Palaeomymar*). Classified in *Mymaromma* are *M. anomalum* (Blood and Kryger) **rev. comb.**, *M. buyckxi* Mathot **rev. comb.**, *M. goethei* Girault **rev. comb.**, *M. mirissimum* (Girault) **n. comb.** and *M. ypt* (Triapitsyn and Berezovskiy) **n. comb.** (all from *Palaeomymar*). Classified in *Mymaromella* is the extinct Tertiary species, *M. duerrenfeldi* (Schlüter and Kohring) **n. comb.**, and the extant species *M. chaoi* (Lin) **n. comb.**, *M. cyclopterus* (Fidalgo and De Santis) **n. comb.** and *M. mira* Girault **rev. comb.** (all from *Palaeomymar*). Classified in *Zealaromma* are the newly designated type species of the genus, *Z. insulare* (Valentine) **n. comb.** (from *Palaeomymar*) and *Z. valentinei* **n. sp.** Description of the structural diversity of extant and extinct mymarommatids is based on the 20 described species plus 15 undescribed extant morphospecies and several fossils from Tertiary Baltic amber and Burmese, Canadian and New Jersey Cretaceous amber. Evidence for monophyly of the genera is presented and the following phylogenetic relationships are hypothesized: *Galloromma* + (*Archaeomma* + (*Zealaromma* + (*Mymaromella* + (*Palaeomymar* + *Mymaromma*))))). Absence of mesotibial and metatibial spurs are newly proposed synapomorphies for Mymarommatoidea. New information is given on the structure of Serphitidae (Serphitoidea) based on study of several Taimyr and Canadian Cretaceous fossils, and structural features that are shared among Serphitoidea, Mymarommatoidea, Chalcidoidea and Platygastroidea are discussed relative to establishing their relationships. Several features, including gastral laterotergites, a mesopectal region similar to a netrion, and a forewing venation that could be ancestral to that of Platygastroidea suggest Serphitoidea is closely related to Platygastroidea. No new evidence was found to support a Serphitoidea + Mymarommatoidea sister-group relationship. Independent parameres in the groundplan of the male genitalia of Mymarommatoidea and Serphitoidea is a likely symplesiomorphy that differentiates them from Chalcidoidea and Platygastroidea. Two different types of specialized claval sensilla could support

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monophyly of Mymarommatoidea + Chalcidoidea, but further study throughout parasitic Hymenoptera is necessary to substantiate character-state distribution and homology.

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The superfamily Mymarommatoidea (Hymenoptera) has been referred to as “arguably the most enigmatic wasp taxon” (Vilhelmsen and Krogmann 2006, p. 290). Individuals are among the smallest of microhymenoptera, only about 0.3–0.8 mm in body length, but Mymarommatoidea is one of the easiest families of Hymenoptera to recognize because of several highly distinctive features. Most conspicuously, the head has a hyperoccipital band of pleated membrane that enables the occipital region to expand and contract in a bellows-like manner, the forewing membrane has a mesh-like pattern, the hind wing is reduced to an apically bifurcate haltere-like structure, and the petiole is composed of two tubular segments (Gibson 1986, Gibson et al. 1999, Vilhelmsen and Krogmann 2006). Partly because of their minute size, mymarommatooids are rarely collected and are poorly represented in most collections, but they have been captured on several subantarctic and Pacific islands (Valentine 1971, Beardsley et al. 2000) and on all continents north into Canada (Clouâtre et al. 1989), Scandinavia (Hansen 1997) and far eastern Russia (Triapitsyn and Berezovskiy 2006). Specimens are also known in Dominican, Sicilian, Baltic, Canadian, Japanese, Taimyr, New Jersey, Burmese, French, Spanish and Lebanese amber, indicating the group has been present for at least 120 million years (Grimaldi and Engel 2005) and has long had a world distribution. Despite their long and apparently ubiquitous presence, almost nothing is known of their biology. Yoshimoto (1984) suggested that they are egg parasitoids, but the life stage they attack and their hosts remain to be discovered. A single individual was reared from a bracket fungus (Gibson 1993) and Huber (1987) noted that most specimens captured in the Northern Hemi-

sphere had been collected in shady and relative moist areas such as deciduous forests. Clouâtre et al. (1989) did extract specimens from forest litter in eastern Canada, but they were also extracted from vegetation litter samples on three subantarctic islands (Valentine 1971). Based on sweep samples, Kryger (cited in Bakkendorf 1948, p. 216) suggested that mymarommatooids are associated with low vegetation and remarked on their “very slow-moving gait — as an old man tired to death”.

Partly because of the lack of comprehensive comparative studies, Mymarommatoidea has a complex nomenclatural history and uncertain phylogenetic relationships within Apocrita. Gibson (1986) and Vilhelmsen and Krogmann (2006) postulated several autapomorphies to support monophyly of the group, but these hypotheses and other character-state knowledge are based primarily on a single European species whose morphology has been studied in detail (Debauche 1948, Vilhelmsen and Krogmann 2006). Knowledge of other mymarommatooid species and genera is limited largely to original descriptions. All 9 previously described extant species and 6 of the 10 extinct species are currently classified in *Palaeomymar* Meunier, 1901, which was established for a species in Baltic amber. Kozlov and Rasnitsyn (1979) stated that the diversity of the fossils they knew from the Cretaceous extended beyond the limits of a single genus, but that it did not seem possible to introduce any clear generic classification without an analysis of all accumulated material. Gibson et al. (1999) also suggested that the extant species could be classified in two genera based on differences in foretibial spur and forewing structure.

The primary purpose of our study is to describe and illustrate the range of mor-

phological variability encompassed by the extant and extinct mymarommatoidea fauna. This is necessary to classify the described species in higher taxa within a phylogenetic perspective and to determine what features are of specific or generic value so that these are included in future descriptions. Our study is also intended to provide the accurate morphological data for Mymarommatoidea necessary for reliable phylogenetic analyses of Hymenoptera. We do not attempt to resolve the higher relationships of Mymarommatoidea within Apocrita because our study of other groups is insufficient for reliable hypotheses of character state homology and distribution. However, we did examine other parasitic Hymenoptera, particularly those groups that have been postulated as closely related to mymarommatoidea, to investigate shared features. We discuss our observations so that the features can be examined more comprehensively for these and other Hymenoptera prior to comprehensive phylogenetic analyses.

## HISTORICAL REVIEW

*Taxonomy.*—Three genera have been established in Mymarommatoidea for extant species: *Mymaromma* Girault (1920), *Petiolaria* Blood and Kryger (1922), and *Mymaromella* Girault (1931). These authors were unaware that Meunier (1901) had established *Palaeomymar* for a mymarommatoidea in Baltic amber that Duisburg (1868) illustrated and discussed but did not name. Although Duisburg did not formally name the species, he gave reasons why he believed it probably belonged to *Mymar* Curtis (Mymaridae). Prior to Meunier, Stein (1877) had discovered a female in Baltic amber that he thought was the same species as the female illustrated by Duisburg and named it *Mymar duisburgi*. Meunier (1901) subsequently examined Duisburg's original amber material and realized that Stein's interpretation of Duisburg's species was incorrect. He reassigned *M. duisburgi* to *Eustochus* Haliday (Mymar-

idae) and established the new genus and species, *Palaeomymar succini* Meunier, based on five males of Duisburg's material. Unaware of either Stein (1877) or Meunier (1901), Bakkendorf (1948) rediscovered Duisburg (1868) and concluded that the illustration seemed to be identical with what Blood and Kryger (1936) had illustrated as the female of *Petiolaria anomala*. Doutt (1973) later synonymised *Mymaromma*, *Mymaromella* and *Petiolaria* under *Palaeomymar*, though he incorrectly cited *M. duisburgi* as the type species of *Palaeomymar*. *Petiolaria* had previously been synonymised under *Mymaromma* by Girault (1930) and *Mymaromella* under *Mymaromma* by Annecke and Doutt (1961). Ever since Doutt (1973), *Mymaromma*, *Mymaromella* and *Petiolaria* have all been considered as synonyms of *Palaeomymar*. Based on our study, we recognize *Palaeomymar* only for *P. succini* and classify all the extant species in *Mymaromma*, *Mymaromella*, and *Zealaromma* **n. gen.** This classification and our newly proposed nomenclatural acts are summarized in Table 1.

In addition to *P. succini* and the extant species, the following extinct species have been classified in *Palaeomymar*: *P. duerrenfeldi* Schlüter and Kohring (1990), *P. japonicum* Fursov et al. (2002), and *P. agapa*, *P. mandibulatus* and *P. senonicus* Kozlov and Rasnitsyn (1979). These species were described from Tertiary and Cretaceous amber deposits spanning about 5–100 mya (Table 1). The other four described extinct species are in three different genera. Yoshimoto (1975) established *Archaeromma* for *Ooctonus minutissimus* Brues, 1937, and his new species, *A. nearcticum*, from Canadian Cretaceous amber. He also described *Protooctonus masneri* from the same material and assigned this taxon to Mymaridae (Chalcidoidea), but we consider that it is a mymarommatoidea (see below). Finally, *Galloromma bezonnaisensis* Schlüter (1978) was established for a specimen from French Cretaceous amber. Based on our study, we classify all the Cretaceous

Table 1. Proposed classification of Mymarommatoidea including temporal and spatial distribution of type material. Abbreviations: E = extant, K = Cretaceous, T = Tertiary; ages based on Grimaldi and Engel (2005).

Classification proposed	Original genus	Temporal and spatial distribution
<sup>†</sup> Gallorommatidae <b>n. fam.</b>		
<i>Galloromma</i> Schlüter, 1978		
<i>agapa</i> (Kozlov & Rasnitsyn, 1979) <b>n. comb.</b>	<i>Palaeomymar</i>	K: Taimyr [Cenomanian (95 mya)]
<i>bezonnaisensis</i> Schlüter, 1978	<i>Galloromma</i>	K: French [Cenomanian (100 mya)]
Mymarommatidae		
<sup>†</sup> <i>Archaeromma</i> Yoshimoto, 1975		
<i>japonicum</i> (Fursov, Shiota, Nomiya & Yamagishi, 2002) <b>n. comb.</b>	<i>Palaeomymar</i>	K: Japanese [Santonian (85 mya)]
<i>mandibulatum</i> (Kozlov & Rasnitsyn, 1979) <b>n. comb.</b>	<i>Palaeomymar</i>	K: Taimyr [Santonian (85 mya)]
<i>masneri</i> (Yoshimoto, 1975) <b>n. comb.</b>	<i>Protooctonus</i> Yoshimoto, 1975	K: Canadian [Campanian (75 mya)]
<i>minutissimum</i> (Brues, 1937)	<i>Ooctonus</i> Haliday, 1833	K: Canadian [Campanian (75 mya)]
<i>nearcticum</i> Yoshimoto, 1975	<i>Archaeromma</i>	K: Canadian [Campanian (75 mya)]
<i>senonicum</i> (Kozlov & Rasnitsyn, 1979) <b>n. comb.</b>	<i>Palaeomymar</i>	K: Taimyr [Santonian (85 mya)]
<sup>†</sup> <i>Palaeomymar</i> Meunier, 1901		
<i>succini</i> Meunier, 1901	<i>Palaeomymar</i>	T: Baltic [Eocene (44 mya)]
<i>Mymaromma</i> Girault, 1920 <b>rev. stat.</b>		
<i>anomalum</i> (Blood & Kryger, 1922) <b>rev. comb.</b>	<i>Petiolaria</i> Blood & Kryger, 1922	E: Britain
<i>buyckxi</i> Mathot, 1966 <b>rev. comb.</b>	<i>Mymaromma</i>	E: Congo
<i>goethei</i> Girault, 1920 <b>rev. comb.</b>	<i>Mymaromma</i>	E: Australia
<i>mirissimum</i> (Girault, 1935) <b>n. comb.</b>	<i>Mymaromella</i>	E: Australia
<i>ypt</i> (Triapitsyn & Berezovskiy, 2006) <b>n. comb.</b>	<i>Palaeomymar</i>	E: Far East Russia
<i>Mymaromella</i> Girault, 1931 <b>rev. stat.</b>		
<i>chaoi</i> (Lin, 1994) <b>n. comb.</b>	<i>Palaeomymar</i>	E: China
<i>cyclopterus</i> (Fidalgo & De Santis, 1882) <b>n. comb.</b>	<i>Palaeomymar</i>	E: Argentina
<sup>†</sup> <i>duerrenfeldi</i> (Schlüter & Kohring, 1990) <b>n. comb.</b>	<i>Palaeomymar</i>	T: Sicilian [Pliocene (5 mya)]
<i>mira</i> Girault, 1931 <b>rev. comb.</b>	<i>Mymaromella</i>	E: Australia
<i>Zealaromma</i> Gibson, Read & Huber <b>n. gen.</b>		
<i>insulare</i> (Valentine, 1971) <b>n. comb.</b>	<i>Mymaromma</i>	E: New Zealand
<i>valentinei</i> Gibson, Read & Huber <b>n. sp.</b>	<i>Zealaromma</i>	E: New Zealand

species in *Archaeromma* and *Galloromma*, and the Tertiary species either in *Palaeomymar* or extant genera (Table 1).

*Classification and relationships.*—Mymarommatids were included in Mymaridae prior to Debauche (1948), who established the family Mymarommidae (*sic*) after a comprehensive morphological comparison of *M. anomalum* with several mymarid genera. Annecke and Doutt (1961) rejected Debauche’s classification and regarded

*Mymaromma* as merely an extremely aberrant mymarid, placing it in the subfamily Mymarinae, tribe Ooctonini. Subsequently, some authors included mymarommatids in Mymaridae (e.g. Valentine 1971, Doutt 1973), sometimes as their own subfamily (Yoshimoto 1975), whereas others treated them as a separate family in Chalcidoidea (e.g. Mathot 1966, Königsman 1978, Yoshimoto 1984). Without explanation, Nikol’skaya (1978) classified *Palaeomymar*

in the otherwise extinct Cretaceous family Serphitidae (Serphitoidea). Kozlov and Rasnitsyn (1979) subsequently provided rationale for this placement based on a single feature shared by the two taxa — a two-segmented petiole. They noted that Yoshimoto (1975) had also described the extinct Canadian Cretaceous genus *Distylopus* (Chalcidoidea: Tetracampidae) as having a two-segmented petiole, but they considered the original description was not sufficiently detailed to establish its systematic position. Gibson (1986) later found that only a single segment formed the petiole of the unique specimen of the type species, *D. bisegmentus* Yoshimoto. He studied petiolar structure as one of 23 adult and larval characters throughout parasitic Hymenoptera and proposed that mymarommatids constituted a monophyletic taxon based on four autapomorphies — head consisting of two plates connected by pleated membrane, hind wing stalk-like with hamuli forming a distal bifurcation, forewing with reticulate pattern, and mesotergal-mesotrochanteral muscle with axillar portion absent. He also proposed that Chalcidoidea, including Mymaridae, was monophyletic based on three autapomorphies and that Chalcidoidea and Mymarommatidae were sister-groups based on three synapomorphies — unique presence of axillar phragmata as sites of origin for all or part of the mesotrochanteral depressor muscles, mesotrochanteral depressor muscle without a mesofurcal or mesoscutal portion, and the male genitalia without an independent basal ring. The last similarity likely is homoplastic because Chiappini and Mazzoni (2000) showed that the male genitalia of some Mymaridae have a distinct basal ring. Regardless, the proposed synapomorphies for Chalcidoidea + Mymarommatidae are all internal and likely never will be informative for testing relationships with Serphitidae because these are known only as amber fossils.

Kozlov and Rasnitsyn (1979) suggested that their new genus *Microserphites* (Ser-

phitidae) was intermediate between Mymarommatidae and Serphitidae because the pronotum did not appear to extend to the base of the forewing, unlike in other serphitids. However, the single specimen constituting *Microserphites* is damaged (top of head and mesonotum not preserved), and the pronotum was described as extending to the tegula in one of their three Cretaceous mymarommatid species. Gibson (1986) suggested that the single unique feature shared between mymarommatids and serphitids, a 2-segmented petiole, likely was derived independently because otherwise members of the two taxa are so dissimilar. Rasnitsyn (1988) subsequently considered the ancestry of mymarommatids as uncertain, being questionably most closely related to either Chalcidoidea or Serphitidae. When Ronquist et al. (1999) reanalyzed Rasnitsyn's data using cladistic methods they recovered Mymarommatidae as the sister group of Chalcidoidea and Serphitidae as either the sister group of Platygastroidea or within a clade that contained Platygastroidea. Rasnitsyn (2002) later included Mymarommatidae and Serphitidae as separate families in Platygastroidea, and these two families as the sister group of Chalcidoidea (Rasnitsyn 2002, fig. 331). This classification more closely reflects the views of Ronquist et al. (1999), but renders Platygastroidea *sensu* Rasnitsyn (2002) paraphyletic. More recently, Rasnitsyn et al. (2004) included Mymarommatidae as one of two families of Serphitoidea, whereas Grimaldi and Engel (2005) treated the families as separate superfamilies. To date, mymarommatids have not been included in published molecular analyses of hymenopteran (Dowton and Austin 2001, Castro and Dowton 2006) or chalcid (Campbell et al. 2000) relationships. Regardless, molecular techniques cannot resolve the question of whether mymarommatids are more closely related to serphitids than to chalcids because serphitids are extinct.

When Gibson (1986) proposed Mymarommatidae as the sister group of Chalcidoidea he left them unplaced to superfamily. He did this because he considered that mymarommatid relationships were ambiguous and because if mymarommatids and chalcids were sister groups then mymarommatids could be included or excluded from “Chalcidoidea” depending on whether internal or external features were used to define that taxon. Noyes and Valentine (1989) first treated mymarommatids as the superfamily Mymarommatoidea, as reviewed by Gibson et al. (1999). The latter authors proposed two additional autapomorphies for the group — mesopleuron, metapleuron and propodeum fused ventral to propodeal spiracle, and propleura and prosternum fused into carapace below pronotum. Most recently, Vilhelmsen and Krogmann (2006) proposed four additional autapomorphies for Mymarommatoidea — absence of a mesothoracic spiracle, fusion of the propleural arm with the profurcal arm, presence of a pair of rods on the anterior surface of the prophragma, and absence of a metafurca.

MATERIALS AND METHODS

*Sources of material.*—This study was based on specimens obtained from the collections listed below. An asterisk indicates the collection included amber material. The names of individuals who facilitated loans of specimens are given in parentheses.

ANIC	Australian National Insect Collection, Canberra, ACT, Australia (John LaSalle, Nicole Fisher).
AMNH*	Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, USA (David Grimaldi).
BMNH	The Natural History Museum, London, England (John Noyes).
BPBM	Bernice P. Bishop Museum, Department of Entomology, Honolulu, HI, USA (John Beardsley).

CIRAD	Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), Montpellier, France (Gerard Delvare).
CNC*	Canadian National Collection of Insects, Ottawa, ON, Canada.
FAUF	Biological Control Research Institute, Fujian Agricultural University, Fuzhou, Fujian Province, China (Naiquan Lin).
GPPC*	George Poinar Personal Collection, maintained at Oregon State University, Corvallis, OR, USA (George Poinar).
GZG*	Geowissenschaftliches Zentrum der Universität Göttingen, Museum, Göttingen, Germany (Mike Reich).
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (Paul Dessart).
MCZ*	Museum of Comparative Zoology, Cambridge, MA, USA (Philip Perkins).
MLPA	Museo de la Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina (Marta Loiacono).
NHRS*	Naturhistoriska riksmuseet, Stockholm, Sweden (Dave Karlsson).
NZAC	New Zealand Arthropod Collection, Entomology Division, DSIR, Auckland, New Zealand (Jo Berry).
PIN*	Palaeontological Institute, Russian Academy of Sciences, Laboratory of Arthropods, Moscow, Russia (Alex Rasnitsyn).
QMBA	Queensland Museum, Queensland Cultural Centre, Brisbane, QLD, Australia (Chris Burwell).
ROMT*	Department of Natural History, Royal Ontario Museum, Toronto, ON, Canada (Janet Waddington).
UCRC	UCR Entomological Teaching and Research Collection, University of California, Riverside, CA, USA (Johan Liljeblad, Jeremiah George, Serguei Triapitsyn, John Heraty).
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (Michael Gates).

ZMB*	Institute of Systematic Zoology, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany (Michael Ohl, Thomas Schlüter).
ZMUC*	Zoological Museum, University of Copenhagen, Copenhagen, Den- mark (Lars Vilhelmsen).

*Techniques.*—The minute size of mymarommatids, the comparatively poor state of preservation of many amber fossils, and the inability to examine body parts of a specimen from all angles in any single amber inclusion prevented us from determining the exact structure and morphological variation encompassed by Tertiary and Cretaceous representatives to the same extent as for extant taxa. For this reason, less complete and comparable descriptions are provided for the extinct genera and a comprehensive description and comparative and functional analysis of extant mymarommatid structure is given prior to discussing the extinct fauna. Character states observed in the fossil taxa are sometimes discussed in the comparative and functional analysis for the purpose of justifying character polarity hypotheses.

The terminology of Basibuyuk and Quicke (1995) is used for the components of the foreleg antenna cleaner, whereas other terms for structure follow Gibson (1997) and Vilhelmsen and Krogmann (2006). The abbreviations used to designate structures in the illustrations are listed in Appendix I. In the text, figure numbers that precede an abbreviation designate figures that have the abbreviation for the relevant structure illustrated, whereas figure numbers following the abbreviation illustrate the structure but do not have these specifically indicated. Our description of the mesosoma is intended to supplement the comprehensive study of the internal and external anatomy of *M. anomalum* by Vilhelmsen and Krogmann (2006) and does not repeat many, normally concealed, anatomical features they described.

We did not locate specimens of the apterous species that Valentine (1971) said he had from mainland New Zealand, which would be important for assessing the effect of wing reduction on mesosomal morphology. Among the material examined, we distinguished 15 morphospecies in addition to the described species (Appendix II). Our study was intended to evaluate morphological diversity rather than formally name species. We therefore describe only one species that is important for phylogenetic inference and for which sufficient specimens are available to interpret structure confidently. Appendix II is given as an aid to locate the specimens we examined and the morphospecies we differentiated for future species descriptions. Many of the specimens are mounted such that features are not visible or directly comparable because of the state of preservation (air *vs.* critical-point dried), method of mounting (card *vs.* point) and/or one body part concealing another. Consequently, an accurate appraisal of the distribution of some character states was not possible and we did not attempt to fully resolve the species limits of *Mymaromma*. Based on variation in intensity of the reticulate pattern of the first petiolar segment, what we interpret as *Mymaromma* sp. 7 may constitute a species complex. Specimens from Taiwan have quite a strongly reticulate first petiolar segment and therefore are very similar to *M. anomalum* and *M. ypt*. The specimens from Taiwan assigned to *M.* sp. 7 were one of three samples of *Mymaromma* for which we had numerous ethanol-preserved individuals; the other two were *M. anomalum* from Sweden and *M.* sp. 6 from Taiwan. Specimens of these three taxa were critical-point dried, dissected, and gold coated for more detailed anatomical study using a Philips XL30 environmental scanning electron microscope (SEM). A single female of *Z. valentinei* was also gold coated for observation, but specimens of the other species were left uncoated as originally mounted on card



points or rectangles. In some instances, the electron beam caused the setae of uncoated specimens to bend (e.g., Figs 55, 71, 144c) so that some images do not accurately reflect setation.

Amber inclusions were examined after the upper surface was covered with a thin film of glycerine and a cover slip. This was done in order to improve visibility through scratches and other minor surface irregularities. In order to obtain an optimal viewing angle, amber blocks were often positioned in a V-like glass well or inserted into a piece of plasticine at the desired angle before glycerine and a cover slip were added. The amber piece was washed subsequently in water to remove the glycerine. After one re-examination of the male paratype of *P. agapa*, the tiny amber shard containing the specimen was lost while it was being transferred to its storage vial by the senior author. The inclusions were examined with a Nikon SMZ1500 binocular microscope using 15x oculars and a 1.6x HR Plan APO objective for a maximum magnification of 270x. When possible, they were examined also with a Nikon Optiphot compound microscope, usually at a magnification of 200x. The binocular microscope had a light base with a mirror for transmitted light, and a halogen spot light and a hand-held fibre optic ring light were used to obtain optimal lighting. Inclusions were photographed with a Leica DC500 digital camera attached to a Leica Z16 APO macroscope or a Nikon E800 compound microscope. The serial images obtained were combined with AutoMontage™ and these and the scanning electron microphotographs were digitally retouched using Adobe Photoshop™ to enhance clarity.

In the original publications, the holotypes of *Galloromma bezonnaisensis* Schlüter (1978) and *Palaeomymar duerrenfeldi* Schlüter and Kohring (1990) were stated as deposited in the "Institute für Paläontologie, Freie Universität, Berlin". These types are now in ZMB.

## EXTANT FAUNA

*Description*.—Body less than 1 mm in length. Body yellow to partly brown without metallic luster, often with a dark brown triangular region or band on mesopleuron below base of forewing (Fig. 82: sa), and tarsal segments often with extreme apices brown; forewing disc sometimes more or less infusate within basal half (Figs 166, 168).

**Head capsule:** Head capsule composed of three parts, a strongly convex anterior or "frontal" plate (Figs 14: frp; 13, 30, 53), a flat, semicircular, posterior or "occipital plate" (Figs 14, 23: ocp; 41, 50), and a ventral "postgenal" plate (Figs 23: pgp; 41, 50). Frontal plate separated dorsally and laterally from occipital plate by pleated membrane originating from above base of each mandible (Figs 13, 14, 53). Occipital plate articulating with postgenal plate along transverse margin above occipital foramen (Figs 23, 41, 50) and capable of rotating anteriorly into head capsule (Fig. 15) or posteriorly beyond vertex in a bellows-like manner (Figs 13, 42). Frontovertex transversely reticulate-scabrous to strigose and sparsely setose (Figs 25, 30, 32, 33, 36, 46, 53). Face usually quite smooth, only very finely striate to strigose (Figs 25, 31, 33, 47, 48), though sometimes with conspicuous mesh-like sculpture (Figs 49, 52, 54); with two "subtorular" setae on midline immediately below toruli (insert, Figs 33, 52) plus 6–12 "interorbital" setae in region between eyes and oral margin (Figs 31, 33, 47–49, 52, 54); oral margin slightly reflexed medially (Figs 25, 33, 56), but clypeus undifferentiated by sutures or evident anterior tentorial pits. Ocelli present (Figs 32, 36, 45, 53) or absent (Figs 25, 30, 33, 46). Toruli subcontiguous and slightly protuberant, at or above level of dorsal margin of eyes (Figs 25, 30, 33, 36). Gena bare except for long seta overlapping base of mandible (Figs 19, 29, 48); malar space variable in length, sometimes long (Figs 47, 52), particularly if eye with few

ommatidia (Fig. 47), but usually short to sublinear (Figs 25, 29, 31, 36, 49) and only rarely with distinct malar sulcus (Fig. 30). Eye variable in size, composed of about 5–55 comparatively large ommatidia (*cf.* Figs 33, 47). Occipital plate with sculpture mesh-like (Fig. 41) to more or less wrinkled-rugulose (Fig. 14); bare except for long seta at extreme ventrolateral corner (Figs 16, 45, 46, 51) and sometimes with a pair of setae paramedially near center (Figs 45, 46: ms); rarely with a ventromedial pit above occipital foramen (Figs 45, 46: opp). Postgenal plate bare except for two long setae laterally in line with ventrolateral seta of occipital plate (Fig. 41), with region between occipital foramen and labiomaxillary complex sclerotized and smooth, the postgenae comparatively widely separated medially (Figs 23, 41, 50). Occipital foramen near dorsal margin of postgenal plate, the orifice surrounded laterally and ventrally by U-shaped region divided by oblique lateral suture (Fig. 24), with single setiform sensillum dorsolaterally, three setiform sensilla ventrolaterally, and with posterior tentorial pits (Fig. 19: ptp) usually visible immediately below ventrolateral sensilla.

**Mouthparts:** Mandible bidentate or tridentate, exodont, their apices not meeting medially when closed (Figs 23, 25, 31, 33, 49, 52), and with 3–5 setae on outer surface, including dorsal seta usually associated with a campaniform sensillum (Figs 27, 34: cs); bidentate mandible with more or less straight dorsal margin ending as acute dorsoapical angulation and with shorter, acute tooth near middle of ventral margin (Figs 34: vt; 47–49, 52, 54); tridentate mandible both with small ventral tooth (Figs 26, 27: vt) and variably distinct dorsal tooth (Fig. 27) or angulation (Fig. 26) extending at least slightly above oral margin (Figs 29, 30: dt). Labrum (Figs 20–22: lbr) thin, flaplike, often convoluted apically, the exposed surfaces smooth (Figs 19–22) but with papillae directed ventrally from inner, ventral surface. Labiomaxillary complex in

ventral view a more or less oval to triangular, flat plate having medial labium (Fig. 20: lab) separated from lateral maxillae (Fig. 20: max) over apical third to two-thirds (Figs 20, 41, 50, 55), and with medial, apparently socketed, papilliform process projecting (Figs 21, 22: pap) externally between labrum and labium. Externally visible part of labium undifferentiated, without palpi, but with pair of setae paramedially near its base (Figs 19–21, 41, 41, 55). Externally visible part of maxilla with long seta laterally near presumptive base; distally differentiated into small subapical lobe (Fig. 41: mxs) bearing terminal spine (Fig. 41: mxp) and longer lateral lobe (Fig. 41: mxg), or with apically narrowed ventral lobe (Figs 21, 57: mxs) bearing spine (Figs 21, 22, 57: mxp) and with dorsal flap (Fig. 21: mxg) or lobe (Fig. 57: mxg) having short, distally projecting papillae (Figs 21, 57) and pustulate surface apically (Figs 20, 21, 22, 57: mxg).

**Antenna:** Antenna geniculate; flagellum without multiporous plate sensilla; first flagellar segment often shorter than second segment but not anelliiform (Figs 171–178). Female antenna 9–11-segmented, distinctly clavate; funicle with 7 (Figs 173: fu; 178) or 6 (Figs 174, 175) segments, the segments progressively more setose toward clava and with unmodified trichoid (hairlike) setae; clava composed of 1 (Figs 173: cl; 174, 175, 178) or 2 (Figs 71, 172: cl) segments, and with at least four different types of sensilla, including trichoid setae on inner and outer surfaces similar to setae of funicle (Figs 58, 72: s1), a few much longer and thicker, usually basally bent sensilla on dorsal or sometimes outer surface (Figs 63, 64, 70: s2), one or more rows of comparatively short and more or less sinuate sensilla on ventral surface (Figs 64, 72: s3), two or three basally bent and slightly lanceolate sensilla, each arising from distinct depression, on outer surface near midline or more dorsally (Figs 62, 63, 70, 71: s4), and often a straight, spine-like sensillum projecting from apex

of clava (Figs 64: as; 65, 67, 69). Male antenna rarely 12-segmented (Fig. 176), usually more (Fig. 171) or less (Fig. 177) distinctly 13-segmented; filiform, but apical 2–4 segments usually somewhat more closely associated or partly fused to form inconspicuously differentiated clava (Figs 60, 61, 66, 68, 73); flagellum relatively sparsely setose, most segments usually with a whorl of long trichoid sensilla medially to subapically (Fig. 171), fl<sub>9</sub> and fl<sub>10</sub> or fl<sub>8</sub>–fl<sub>10</sub> each with a basally bent, slightly lanceolate sensillum arising from distinct depression distally (Figs 60, 66, 68: s4; 61, 73), and apical segment with spine-like sensillum projecting from apex.

**Mesosoma:** Pronotum in dorsal view not visible (Figs 78, 79), very short and vertical medially (Fig. 111). Pronotum in lateral view triangular with acute posterodorsal angle extending almost to base of forewing (Figs 80, 103), with single seta posteriorly near dorsal margin (Fig. 80); dorsal and posterior margins often appressed to lateral margin of mesoscutum and anterior margin of mesopleuron, respectively (Figs 80, 95, 96, 101, 108), but not rigidly connected by tongue and groove interlocking system so that posterior margin often displaced from anterior margin of mesopleuron over dorsal third to half (Figs 13: am; 53, 82, 97, 99); posterior margin sometimes with distinct notch (Figs 16, 82: pn; 99, 101) near dorsal quarter, but without evident spiracle. Pronotum in ventral view not continuous between sides (i.e., not annular) (Fig. 86). Propleura forming entire lateral and ventral surfaces of propectus (Fig. 86), divided mediolongitudinally (Figs 43, 112) or more or less extensively and indistinguishably fused medially (Figs 18, 44, 86). Prosternum reflexed internally at about 90 degrees to posterior margin of propleura, comprising a transverse, vertical surface largely concealed between propleura and base of procoxae (Vilhelmsen and Krogmann 2006, fig. 8). Prepectus not visible externally. Tegula absent, but base of forewing

with bare, oval, humeral plate (Figs 82, 101: hp) resembling a tegula. Mesoscutum (Figs 45, 78, 79, 91, 93) scabrous, without evident notauli or parapsidal lines, and bare except for four long setae posteriorly in a transverse line; transscutellar articulation straight-transverse. Scutellum (Figs 45, 78, 79, 91, 93, 109) in dorsal view without differentiated axillae, consisting of convex, more or less hourglass-shaped (i.e., lateral margins incurved) anterior scutellum and transverse, concave posterior scutellum (frenum) (Figs 78, 79, 91, 93). Anterior scutellum in dorsal view scabrous to longitudinally scabrous-strigose, but bare except for seta on either side within anterior half (Figs 79, 108, 109); in lateral view, the almost vertical side finely sculptured (Figs 91, 93, 97, 109). Posterior scutellum more or less distinctly, longitudinally strigose (Figs 78, 79, 91, 93, 109). Mesopleuron high-rectangular with anterior margin reflexed as slender rim (Figs 13: am; 82, 97) normally concealed by posterior margin of pronotum; dorsal margin with three setiform “subalar” sensilla below base of forewing (Fig. 98: sas); without differentiated mesepisternum and mesepimeron, and distinct subalar area (acropleuron) not differentiated except often by colour difference described above. Metanotum dorsomedially slender and more or less concealed under posterior margin of scutellum (Figs 78, 84: no<sub>3</sub>; 79, 91, 93, 97, 99, 101); laterally separate from metapleuron and propodeum (Fig. 105: no<sub>3</sub>, pl<sub>3</sub>, pro) or fused with metapleuron (Fig. 84: no<sub>3</sub>, pl<sub>3</sub>), propodeum (Figs 102: “no<sub>3</sub>”, pro; 97, 98, 100), or both metapleuron and propodeum (Figs 109, 110: “no<sub>3</sub>”). Meso- and metapleuron completely fused (Figs 80, 83, 103, 108) except for short suture below base of wings (Fig. 80: mms) or partly (Fig. 87: mms) to completely separated by oblique suture (Figs 82: mms; 95–97, 99, 101); bare, variable in sculpture. Meso/metapleural complex, when separated by suture, often with suture slightly widened or posterior mar-

gin of mesopleuron with tiny notch (Figs 97, 98: mn) dorsally at same level as notch on posterior margin of pronotum. Meso/metapleural complex, when fused, usually with variably distinct, curved groove (paracoxal sulcus *sensu* Vilhelmsen and Krogmann 2006, fig. 1) extending from intersegmental pit (Fig. 80: isp) to metapleural pit (Figs 80–82, 87: pl<sub>3</sub>p) or propodeal spiracle (Figs 103, 108), and rarely with very tiny pit (Fig. 87: pl<sub>2</sub>p) at height similar to metapleural pit (Fig. 87: pl<sub>3</sub>p). Metapleuron indistinguishably fused with propodeum except usually above propodeal spiracle (Figs 80, 82–84, 97–102); without (Figs 95, 96, 99, 103, 108) or with variably distinct metapleural pit (Figs 80–82, 87, 97, 101: pl<sub>3</sub>p); dorsal margin with a single setiform sensillum near base of hind wing (Figs 85, 98, 105, 110: dms); anteroventral corner often projecting slightly anteriorly to abut reflexed rim of slightly projecting mesocoxal foramen (Figs 86, 87) (in lateral view the two protrusions usually form a pit (Figs 80, 86: isp) between them). Metathoracic-propodeal complex with single setiform or digitiform “postalar sensillum” (Figs 84, 85, 98, 100, 102, 105, 110, 127: pas), almost always with two setiform “prespiracular sensilla” (Figs 84, 85, 98, 110, 127: pss; 100, 105), and usually with one, or rarely two, “suprapleural” setiform sensilla (Figs 85, 98: sps) anterior to postalar sensillum between dorsal margin of metapleuron and ventral margin of scutellar-axillar complex. Propodeum with sculpture variable, more or less reticulate to transverse-strigose at least dorsally (Figs 78, 79, 91, 93, 107); with single seta near posterior margin of spiracle (Figs 84: prs; 80–83, 95–102, 105, 109); posteriorly reflexed into variably distinct and high flange (Figs 92, 94, 104: pf) on either side of short foraminal tube (Figs 90–97, 99, 101, 103, 104, 107) or into continuous  $\cap$ -like flange encircling petiolar insertion dorsally and laterally (Figs 81, 87: pf) (in either instance the flange and dorsal rim of metacoxal foramen abut to

form pincer-like structure surrounding deep pit (Figs 80, 86: isp; 104, 108)). Propodeal spiracle (Figs 84, 100, 105, 109: sp) below level of propodeal surface, surrounded by spiracular aperture (Figs 84, 100, 105, 109: spa); spiracular aperture usually circular to oval (Figs 80, 84, 100, 105, 109: spa), rarely slit-like (Fig. 82: spa), and usually continuous to anterolateral margin of propodeum as deep slit (spiracular peritreme) (Figs 80, 82, 84, 100: spp), with the peritreme and dorsal margin of metapleuron either forming acute angle (Figs 82–84) or more uniformly convex margin (Figs 97–102).

**Wings:** Forewing pedunculate (Figs 163–166, 168) with more or less lanceolate to broadly spatulate disc (Figs 113, 124: dsc) and slender basal stalk (Fig. 124: stk). Forewing disc sometimes almost flat (Fig. 166), but usually more or less distinctly convoluted by series of longitudinal folds (Figs 163, 164); without venation but with raised lineations on both upper and lower surfaces of membrane forming a double layered mesh-like pattern interior to level of insertion of marginal setae (Figs 123, 163–165); discal setae varying from short and spine-like (Fig. 166) to long and hair-like (Figs 163, 164), sometimes appearing dense when very long (Fig. 116), but aligned in row along folds when disc convoluted (Figs 163, 164); marginal setae, when long, arising distinctly from within periphery of apical portion of disc (Figs 163, 165, 168). Forewing stalk (Fig. 124: stk) more or less distinctly subdivided into “proximal” and “distal” portions, the distal part consisting of strongly narrowed base of disc (Fig. 124: std). In dorsal view, proximal part of stalk (Fig. 124: stp) differentiated into convex, anterior and posterior longitudinal bands separated by furrow over most of length except basally (Figs 127, 134); posterior band bare but anterior band with sparse, short spicules at least anteriorly and with a campaniform sensillum distally (Figs 125, 126, 128: cs) near base of long

seta (Figs 125–128: mc). In ventral view, proximal part of stalk with at least basal half of anterior margin folded under wing as basally widened region of membrane (Figs 129, 132: cc), the membrane with scattered spicules (Figs 129, 132) or these sometimes in row (Figs 95, 130) and, at least sometimes, with a campaniform sensillum basally to medially (Figs 132, 135: cs), and with non-folded portion differentiated into anterior band having short spicules and concave trough along posterior margin (Figs 130, 132: ret). Hind wing with bulbous base (Fig. 136) and slender stalk terminated by pincer-like structure; stalk with two or rarely three subbasal setae and one medial to subapical seta on anterior margin (Fig. 136), and sometimes with a slender band of membrane posteriorly (Figs 135, 136: mb), the membrane sometimes also with single short seta (Fig. 135); apical pincer formed by socketed hamulus (Fig. 135: ham) and slender projection opposite to hamulus (Figs 134, 135: op), the projection and sometimes also the hamulus apically bifurcate (Figs 134–136).

**Legs:** Meso- and metacoxae with basicoxite reduced to a small lobe (Figs 81, 104, 107: bc) inserted into widely separated foramina (Fig. 86). Femora with differentiated trochantellus; posterior surface of femora sometimes with small bumps (Fig. 146). Tibial spur formula 1:0:0. Prothibia without row of modified setae (secondary fine comb) along anterior margin apically; calcar curved and apically bifurcate (Figs 137, 138, 139a, 140: ca) or straight and simple (Figs 142, 144a, 145a: ca); mesotibia ventroapically with two strong, apically divergent, socketed setae projecting distally from tube-like elevations of cuticle (Figs 139b, 141b, 144b: ps); metatibia with strong setae originating from cuticular protrusions ventroapically (Figs 139c, 141c, 144c: ps) and anteroapically (Figs 139c, 144c). Tarsi 5-segmented; protarsus with fine comb of basitarsus (Figs 137: fc; 140, 143, 145a) aligned longi-

tudinally, the lanceolate setae slightly flattened and differentiated in length so apices form a concave arc.

**Metasoma:** Metasoma 8-segmented, the basal two segments tubular, hence with 2-segmented petiole (Figs 83, 104: pt<sub>1</sub>, pt<sub>2</sub>; 88, 92, 94). First petiolar segment almost smooth (Figs 81, 83, 104, 107), transversely strigose (Figs 90, 92–94) or reticulate (Fig. 88), and often with single seta on either side in anterior half (Figs 92, 94, 104, 107). Second petiolar segment finely sculptured dorsally and often with tiny spicules (Fig. 83, insert) or transversely strigose (Figs 92, 94). Post-petiolar segments (= gaster) of air-dried specimens usually flattened-oval in cross-section, but terga broadly overlapping sterna laterally (i.e., without differentiated laterotergites), and smooth and shiny (Fig. 147); without spiracles except usually on Mt<sub>7</sub> (Figs 149: sp; 150–152, 158, 159). Gaster (Fig. 147) in dorsal view with posterodorsal margin of Mt<sub>3</sub> broadly and deeply incurved and Mt<sub>4</sub> the largest tergite; Mt<sub>3</sub> with two to several setae dorsolaterally near anterior margin; Mt<sub>7</sub> with single seta near spiracle (Figs 149–152) or usually paralaterally when spiracle absent (Fig. 154); syntergum (Mt<sub>8+9</sub>) with 2–4 setae in row near posterior margin (Figs 150, 152, 153, 155) and usually with cerci (Figs 150, 152: cer; 149, 151, 158), the cercus usually flat or low convex, subcircular, differentiated from tergite by distinct groove, and bearing 1–4 long setae (Figs 150, 151, 158), but sometimes partly fused with tergite or apparent only as subcircular depression (Fig. 152). Hypopygium of female (Fig. 148: hyp) with several setae apically (Figs 148, 149, 153), the sclerite extending almost to apex of metasoma and concealing ovipositor when appressed to syntergum (Fig. 148: syn), but apex capable of separating widely from syntergum (Figs 149: syn; 147, 153) for ventral rotation of ovipositor (Figs 152, 153: ov; 147, 149). Hypopygium of male bare, but with a campaniform sensillum laterally near base (Fig. 160: cs). Male

genitalia without basal ring or phallobase, consisting of large medial aedeagus (Figs 154, 155, 158, 160: aed), ventrolateral volsellae with digiti (Figs 160, 162: vol, dig), and sometimes with externally protruding parameres (Figs 154, 156: par; 155). Aedeagus in dorsal view (Fig. 158) divided apically and distinctly bilobed basally, with basal lobes much smaller and more slender than posteriorly broadened apical lobes and each basal lobe with small pit near its anterior margin; in ventral view gonopore positioned apically (Fig. 160: gp); internally with paired apodemes extending anteriorly (Figs 169, 170: aea). Volsella (Figs 160, 162: vol) extending anteriorly into body as slender apodeme (Figs 169, 170: voa) and posteriorly broadened into a digitus (Figs 161, 162: dig) having one or two short spines (Figs 161, 162: dis), the two volsellae together forming a posteriorly directed, Y-shaped structure. Paramere, when present, projecting externally from between syntergum and hypopygium lateral to aedeagal-volsellar complex as elongate-digitiform process with a long terminal seta (Figs 154, 156: par), and extending internally as rod-like structure (Fig. 169: paa) articulating with genital complex basal to volsellar apodemes.

*Comparative and functional morphology.*—

**Head capsule:** Certainly the most bizarre structural modification of extant mymarommatids is their unique “bellows-like” head (Figs 13, 42). The functional significance of this remains uncertain, but Cretaceous fossils suggest that origin of a hyperoccipital band of pleated membrane and a moveable occipital plate likely evolved concurrently with exodont mandibles. If mymarommatids are egg parasitoids it is possible that the adult emerges from the host egg by opening its exodont mandibles and rupturing rather than chewing the chorion. Expansion of the occipital region to enlarge the head (*cf.* Figs 13, 14) may serve to fill the enclosing space so that the mandibles are appressed firmly against the chorion. By doing so, the mandibles are

more likely to break the membrane rather than simply pushing the head away from it when they are opened outwards. Such an hypothesis does not explain why the occipital plate can also rotate deeply within the head capsule (Fig. 15), unless this is merely an artifact of drying made possible by the bellows-like structure.

The seemingly ventral position of the occipital foramen on the head (Figs 14, 15, 45, 53) is a consequence of the modified head structure. The occipital foramen actually is near the center of the head, as in other hymenopterans, but it appears to be more ventral because the posterior surface of the head is abruptly angled along a transverse axis near the dorsal margin of the occipital foramen (Figs 23, 41, 50). This angulation serves as the hinge that allows the occipital plate to rotate anteriorly (Fig. 15) and posteriorly (Fig. 13) relative to the frontal plate. The structure of the occipital foramen and the region between the foramen and labiomaxillary complex appears to be quite consistent across the family (Figs 23, 24, 41, 50), though we examined this in detail for very few species.

Many species have the frontal plate more coarsely sculptured ventrolaterally near where the hyperoccipital band of pleated membrane originates than immediately posterior to the eye (Figs 29, 30, 54). The sculpture is developed as short vertical ridges in some species and specimens of *M. anomalum* from Sweden have a small series of ridges or denticles ventrolaterally on both the frontal and occipital plates (Figs 16, 17). The denticles interdigitate when the occipital plate is vertical relative to the frontal plate (Fig. 17) and together they may serve as a weak locking mechanism to align the occipital and frontal plates and to inhibit rotation of the occipital plate. The exact distribution of such interlocking denticles is not known, but most species apparently lack them (Figs 42, 45, 51, 53). All examined species have a single seta ventrolaterally on the

occipital plate that typically projects somewhat over the hyperoccipital band of pleated membrane (Figs 15, 16, 41, 51). This seta likely serves to sense whether the occipital plate is rotated within the head capsule. A long seta on the gena and the ventral-most seta of the postgenal plate also overlap the base of the mandible (Figs 19, 35). These setae likely serve to sense when the mandible is opened.

The only head capsule feature of extant mymarommatids that appears to be of generic value is the presence or absence of paramedial setae on the occipital plate. Species of *Mymaromella* have a pair of setae (Figs 45, 46: ms), whereas those of *Mymaromma* and *Zealaromma* do not. All examined mymarommatids have two subtorular setae (Figs 33, 52, insert), but they differ in the number and pattern of interorbital facial setae (cf. Figs 25, 31, 33, 47–49). Both species of *Zealaromma* have four interorbital setae above the oral margin (Fig. 56). There are only two interorbital seta above the oral margin in *Mymaromma* (Figs 18, 20), but species of *Mymaromella* either have two or four such setae. Both species of *Zealaromma* share a distinctive facial sculpture (Figs 52, 54), but a few species of *Mymaromella* also have distinct facial sculpture (Fig. 49). Other features such as the presence or absence of ocelli and relative size of the eyes and number of ommatidia are even more variable among species.

**Mouthparts:** The exodont mandibles of *Zealaromma* (Figs 52, 54) and *Mymaromella* (Figs 47–49) are bidentate and comparatively gracile except in *Mymaromella* sp. 23. The single known female of this species uniquely has large, robust mandibles with-in a conspicuously large oral orifice (Figs 36, 37, 39). Because the left mandible is open its inner surface is visible (Figs 36, 37: i). The inner surface is smooth with one dorsoapical and one dorsomesal seta and two campaniform sensilla, one below the dorsomesal seta and one ventromesally (Fig. 37: cs). The relative position of the two mandibles show that a mandible is

rotated as it is opened so that the “dorsal” surface of a closed mandible projects laterally when open (Figs 36, 37: d) and the “outer” surface becomes “ventral” (Fig. 37: o). The “dorsal” surface (Fig. 40: d) is slightly concave, has two small, outcurved teeth apically, and two setae basally, one adjacent to a campaniform sensillum (Fig. 40: cs). The outer surface (Fig. 37: o) is flat, has three setae, and its apical margin is quite long, almost vertical, with a knife-like edge (Fig. 37: c). We infer that the dorsal surface of the mandible in its closed position in *M. sp. 23* is homologous with the external surface of the mandible of other mymarommatids because it is concave with two teeth and has a seta associated with a campaniform sensillum. We did not observe a campaniform sensillum associated with a dorsal seta on the outer mandibular surface in all mymarommatids examined, but based on wide distribution of the sensillum we suspect that this was because the mandible was not clean enough for it to be observed rather than it being absent. In species of *Mymaromella*, the campaniform sensillum usually is within the depression from which the dorsal seta arises and therefore can be observed only under some angles (cf. Figs 34, 35: cs). Similarly, we are not certain whether a second, more mesal campaniform sensillum evident on the outer mandibular surface in some species (Fig. 35) is characteristic of all species and genera, or whether campaniform sensilla are characteristic of the internal surface of all mymarommatid mandibles.

The mandibles of most species of *Mymaromma* differ from those of *Mymaromella* and *Zealaromma* because each has an additional dorsal angle (Figs 25, 26) or tooth (Figs 19, 27, 28) that projects above the oral margin, at least slightly (Figs 29, 30: dt). The only known exception is *Mymaromma* sp. 9, which has bidentate mandibles (Fig. 31). The mandibles of some species of *Mymaromella*, if viewed slightly from below, sometimes appear to



have a very tiny dorsal tooth (Fig. 44), but this is the base of the socketed seta at the dorsal margin of the mandible and it does not project above the oral margin when viewed anteriorly (Fig. 48).

The labiomaxillary complex of mymarommatids is strongly reduced, which makes definitive homology of its components with those of other parasitic Hymenoptera uncertain. Extant mymarommatids have a ventral labiomaxillary plate composed of a medial labium (Fig. 20: lab) and lateral maxillae (Fig. 20: max) that are fused together over at least their posterior third. The externally visible part of the labium we interpret as the prementum (Fig. 21: lpm). A medial papilliform process (Figs 21, 22: pap) also projects externally from between the labrum and labium. Except for *Mymaromma* sp. 9 (Fig. 31, insert), the labium is much wider in species of *Mymaromma* (Figs 18–21, 23, 28) than in *Mymaromella* (Figs 41, 41, 44, 48, 49) and *Zealaromma* (Figs 50, 52, 55, 56). Because of the condition of available specimens we could not determine the exact structure of the maxilla in *M.* sp. 9. In other species of *Mymaromma* and in *Zealaromma* the maxilla often appears to be composed of a single lobe terminated by a spine (in *Zealaromma* the lobe projects slightly on either side of the base of the spine, Figs 56, 57), but there is also a second fleshy lobe above the ventral lobe of the maxilla. This dorsal maxillar lobe appears flat when the labiomaxillary complex is appressed to the head capsule (Fig. 21: mxg) and more tubular when the complex is distended (Fig. 57: mxg). When the dorsal maxillar lobe is expanded, oblique rows of distally projecting papillae are visible in lateral view (Fig. 57), which appear as dorsally projecting papillae when the lobe is flattened (Fig. 21). Furthermore, the dorsal lobe is differentiated apically as a pustulate lobe (Figs 20–22, 56, 57) that projects slightly beyond the terminal spine of the ventral maxillar lobe. Species of *Mymaromella* have a slightly different maxillar structure be-

cause the spine-like process (Fig. 41: mxp) originates from a small lobe (Fig. 41: mxs) on the inner side of a longer fleshy lobe (Fig. 41: mxg), which in at least some species has distally projecting papillae on its upper/outer surfaces (*cf.* Fig. 57). We consider that the small subapical lobe bearing the spine is a remnant of the maxillary palpus (Fig. 41: mxp), the inner surface from which it arises as likely a remnant of the stipes (Fig. 41: mxs), and the longer outer lobe as likely a remnant of the galea (Fig. 41: mxg). We also consider the thin, apically pustulate lobe above the stipes in *Mymaromma* and *Zealaromma* as a more internalized galea (Figs 21, 22, 57: mxg), i.e., homologous with the outer lobe of the maxilla in *Mymaromella*. The structural homology of the papilliform process that projects externally between the labrum and labium (Figs 21, 22: pap) is uncertain, though it might be the hypopharynx or a part of the maxilla (possibly the ligula).

Our interpretation of the labiomaxillary complex differs from that of Debauche (1948, fig. 16a), who considered that the maxillary stipes were fused medially so that they completely covered what we interpret as the prementum of the labium (Fig. 21: lpm). He also considered the long posterolateral setae of the labiomaxillary complex as the maxillary palpi. The two very similar paramedial setae he considered simply as sensory hairs. The maxillary regions in *Mymaromma* that we consider as the stipes he interpreted as the galea.

The structure of the labiomaxillary complex was not visible in most fossil mymarommatids we examined, but a paratype of *Palaeomymar senonicus* clearly has the labium only about as wide as the maxillae and these apparently separated for most if not all of their length (Fig. 203). We could not determine the presence of maxillary or labial palpi.

**Antenna:** For this study we included what Beardsley et al. (2000) identified as an unnamed species from Hawaii near *Mymaromma goethei* in *M. goethei* (Appen-

dix II). Females we include in *M. goethei* have six (Figs 174, 175) rather than seven funicular segments. We also saw one female of *Mymaromella* sp. 6 that has seven funicular segments in one antenna and six segments in the other. Males we identify as *M. goethei* from Australia and Hawaii have 12-segmented antennae (Fig. 176). The males of other species have 13-segmented antennae (Figs 171, 177), though the apical two segments sometimes are only indistinctly separated (Fig. 177). We suggest that the 12-segmented antenna of male *M. goethei* and what is either the same or a very similar species in Hawaii results from the loss of a funicular segment, as for females, rather than the loss of the apical claval segment.

Male mymarommatids lack the s2-type and s3-type sensilla present on the clava of females, but both sexes have s4-type sensilla. The latter sensilla are more or less lanceolate in shape, are directed apically because they are strongly bent basally, and each originates from a distinct circular depression (Figs 58, 60, 62, 64, 66, 68, 70, 71: s4). Females of *Mymaromma* and *Zealaromma* have two s4-type sensilla and females of *Mymaromella* two or three such sensilla on the outer surface of the clava. Both sensilla are on the apical claval segment in *Zealaromma* (Fig. 71). The sensilla are near the dorsal margin of the clava in *Mymaromma* (Figs 58, 59) and *Zealaromma* (Fig. 71), but near the midline or even more ventrally in *Mymaromella* (Figs 62, 63, 65, 67, 69). Males lack s4-type sensilla from the apical flagellar segment, but the preceding two or three segments have a single s4-type sensillum distally depending on whether the female of the species has two or three such sensilla on the clava (cf. Figs 65 and 66, 67 and 68, 71 and 73). We observed strong, basally curved sensilla projecting from the outer or dorsal surfaces of the clava of some Cretaceous females, but are uncertain whether they are s2-type or unusually long s4-type sensilla.

**Mesosoma:** The internal and external mesosomal structure of *Mymaromma anomalum* was studied comprehensively by Vilhelmsen and Krogmann (2006). They noted that in *M. anomalum* the propleura and prosternum are fused, except for a short distance anteriorly, so that there is a continual ventral "carapace" (Vilhelmsen and Krogmann 2006, fig. 6; cf. Figs 18, 86). Because of the fusion they were uncertain as to their original structure. Our survey demonstrated that both species of *Zealaromma* (Fig. 112) and at least some fossil mymarommatids have medially abutting propleura (not visible in all inclusions). We could not observe this feature in all examined species of *Mymaromella* and *Mymaromma*, but species of *Mymaromella* appear to have medially abutting propleura or at least a sulcus or differentiated line of sculpture along the ventral midline (Figs 43, 44), whereas species of *Mymaromma* have an undifferentiated carapace similar to *M. anomalum*.

Vilhelmsen and Krogmann (2006) showed that the mesothoracic spiracle and an externally evident prepectus were missing from *M. anomalum*, but stated that it would be desirable to establish position of a spiracle relative to the prepectus for inferring possible sister-group relationships of mymarommatids. They also noted that the pronotum had a notch in its posterior margin at about one third of its height from the dorsal margin (Vilhelmsen and Krogmann 2006, fig. 1), but did not comment that this position is similar to that of the mesothoracic spiracle in most parasitic Hymenoptera other than the Chalcidoidea. Our survey shows that all mymarommatoids lack a mesothoracic spiracle and an external prepectus, but that there is a pronotal notch in many *Mymaromma* (Figs 16, 82: pn) and *Mymaromella* (Figs 97, 99, 101). We did not observe a pronotal notch in *Zealaromma* (Figs 103, 108) or any Cretaceous representative, though the lateral structure of the pronotum was not clearly visible in many amber inclusions.

Vilhelmsen and Krogmann (2006) further stated that the pronotum is rigidly associated with the mesopleuron in *M. anomalum*. Our survey showed that the pronotum extends to the mesopleuron ventrally in mymarommatids and does not appear to be moveable relative to the mesothorax, but in many species and specimens the posterior margin is separated from the mesopleuron over its dorsal third to half (Figs 13, 82, 97, 99). Vilhelmsen and Krogmann (2006) also described and illustrated an internal structure near the posterior margin of the pronotum that they postulated was the prepectus fused to the pronotum. Our study did not include internal features, but we concur with their interpretation that the structure parallel to the posterolateral margin of the pronotum (Vilhelmsen and Krogmann 2006, fig. 4) likely is the prepectus. They concluded that the structure is fused with the pronotum. If so, it is not homologous with a posterolateral pronotal inflection *sensu* Gibson (1985). Remnants of membrane on the dorsal and posterior margins of the putative prepectus (Vilhelmsen and Krogmann 2006, figs 4, 5) suggest that this is where membrane from the mesoscutum and anterior margin of the mesopleuron attach, respectively, providing the pronotum with the flexibility to be separated from the mesopleuron dorsally (Figs 13, 53, 82, 97, 99) but at the same time retaining structural continuity between the pronotum and mesothorax. Even if separation of the pronotum from the mesopleuron dorsally is only an artifact of drying, their separation shows their margins are not rigidly interlocked by a tongue and groove mechanism as in taxa with a posterolateral pronotal inflection.

Vilhelmsen and Krogmann (2006) noted that the mesopleuron and metapleuron are fused together in *M. anomalum*, which was hypothesized as an autapomorphy of Mymarommatidae by Gibson et al. (1999). Our survey shows that the meso- and metapleura are separate sclerites in *Mymarom-*

*mella* (Figs 95–99, 101) and in those fossil taxa where the feature is visible. Except for a very short distance immediately below the hind wing (Fig. 80: mms), the sclerites are fused in *Zealaromma* (Figs 103, 108) and in most *Mymaromma*. *Mymaromma* sp. 9 has the meso- and metapleura completely separated (Fig. 82: mms) and they are separated over about their ventral half in *Mymaromma* sp. 7 (Fig. 87: mms). In *Mymaromella*, there is often a tiny notch in the posterior margin of the mesopleuron (Figs 97, 98: mn) or a slight widening of the suture between the meso- and metapleuron at a similar height as the notch on the pronotum. Based on this positional similarity, the notch on the posterior margin of the mesopleuron could be a remnant of the metapleural spiracle.

The dorsal surface of the mesosoma of mymarommatids we examined is very similar to that described for *M. anomalum* by Vilhelmsen and Krogmann (2006) except for species-specific sculptural differences. However, structure of the metathoracic-propodeal complex differs conspicuously among *Mymaromma*, *Mymaromella* and *Zealaromma*. As described by Vilhelmsen and Krogmann (2006), the aperture of the propodeal spiracle continues as a slender peritreme dorsally to the anterior margin of the propodeum in *M. anomalum* (cf. Fig. 84: spp). The spiracular aperture (Figs 80, 82, 84, 100, 105: spa) is the more or less enlarged ventral portion of the spiracular peritreme that overlies the actual opening of the propodeal spiracle (Figs 84, 100, 105, 109: sp). They interpreted the spiracular peritreme as the antecostal suture, which separates the metanotum from the propodeum. A slit-like spiracular peritreme is characteristic of both *Mymaromma* and *Mymaromella*, but its direction differs in the two genera and this determines whether the postalar sensillum and prespiracular sensilla appear to be located on the metathorax (Fig. 84: pas, pss) or on what appears to be the anterolateral angle of the propodeum (Fig. 98:

pas, pss). In *Mymaromella*, the spiracular peritreme is directed anterodorsally and the metanotum and propodeum are fused mesal to the spiracular peritreme, though sometimes a carina is present that may represent the line of fusion (Figs 98, 102: c). Consequently, a slit separates the dorsal margin of the metapleuron from the lateral margin of the metanotum/propodeum and in lateral view the peritreme and dorsal margin of the metapleuron together form a relatively evenly convex arc (Figs 97–102). The prespiracular sensilla (Figs 98: pss; 100, 102) are on the metanotum/propodeum above the spiracle and the postalar sensillum is anterior to these, often also obviously on the metanotum/propodeum (Fig. 98: pas). However, this position for the postalar sensillum is not so obvious in species that have the anterolateral angle of the metanotum/propodeum narrowly attenuated (cf. Figs 99, 100), and in *M. sp. 17* the sensillum appears to be disassociated from the metanotum/propodeum (Fig. 102: pas). *Mymaromella sp. 17* is the only mymaromatid we observed having a single prespiracular sensillum (Fig. 102), though this observation is based on only a single clean specimen. Additional individuals are required to determine whether the number of prespiracular sensilla are variable in *M. sp. 17* or the loss of one sensillum is correlated with what appears to be a more highly reduced “metanotum” in this species (Fig. 102: “no<sub>3</sub>”). In *Mymaromma*, the spiracular peritreme is directed dorsally, apparently continuous with the antecostal suture, and the metanotum and metapleuron are fused together to form a single  $\cap$ -like sclerite anterior to the peritreme (Fig. 84). In lateral view, the peritreme and dorsal margin of the metapleuron converge dorsally to form an acute angle (Figs 82–84), and the prespiracular sensilla are on the metathorax near the presumed line of fusion between the lateral margin of the metanotum and dorsal margin of the metapleuron (Fig. 84: pss). The postalar sensillum (Fig. 84: pas) ap-

pears to originate from the dorsal margin of the metapleuron anterior to the prespiracular sensilla. In very clean specimens (Fig. 85: no<sub>3</sub>?; Vilhelmsen and Krogmann 2006, fig. 11), the sensillum is seen to originate from a small, more or less triangular region that is differentiated above the dorsal margin of the metapleuron. The posterior edge of the differentiated region projects slightly so that the postalar sensillum sometimes appears bilobed (Vilhelmsen and Krogmann 2006, fig. 11).

The different locations of the postalar and prespiracular sensilla in *Mymaromma* and *Mymaromella* show that their different metathoracic-propodeal structures are not a result of a simple shift in direction of the spiracular peritreme, and that one propodeal structure was not derived directly from the other. If the peritreme simply shifted direction this should not affect position of the sensilla on the body relative to the different sclerites.

The metanotum or the anterodorsal angle of the metanotum/propodeum appear to be separated quite widely from the base of the hind wing in *Mymaromma* (Figs 83, 84: hwb) and often in *Mymaromella* (Figs 95, 101, 102), though sometimes in *Mymaromella* there actually is a slender, inconspicuous intervening region (Fig. 100). The metanotum in other Hymenoptera, including Mymaridae, is more or less truncate laterally (Fig. 11: no<sub>3</sub>). Typically, the metanotum extends to the inner margin of the base of the hind wing and the anterodorsal margin of the propodeum extends to the posterior margin of the hind wing (Fig. 11: no<sub>3</sub>, hwb, pro). In Mymaridae, there are setiform sensilla at the extreme anterolateral angle of the propodeum below the base of the hind wing (Fig. 11). Furthermore, the mymarid metanotum (Figs 11, 12) typically has a single seta near its anterior margin sublaterally and three more lateral setae, one of the setae being somewhat more medial than two setae at the extreme lateral margin of the metanotum. In some mymarids, such

as *Mymar*, the somewhat more medial seta originates from the inner surface of the metanotum (Fig. 12). *Mymaromatids* do not have a sensillum in the position of the sublateral metanotal seta of mymarids, but at least some have one, and apparently sometimes two, setiform suprapleural sensilla (Figs 85, 98: sps) between the metapleuron and scutellar-axillar complex anterior to the postalar sensillum. We postulate that the prespiracular sensilla (Figs 84, 85, 98, 101, 102: pss) in mymaromatids are of metanotal origin based on their positional homology with similar sensilla in mymarids (Figs 11, 12). We also postulate that the postalar sensillum is of metanotal origin because of its position in most *Mymaromella* (Figs 98, 100: pas). Although the postalar sensillum appears to originate from the dorsal margin of the metapleuron in *Mymaromma* (Fig. 84: pas), we suggest that the thickened region from which it originates (Fig. 85: no<sub>3</sub>?) actually is lateral remnant of the metanotum that remains near the base of the hind wing (Fig. 84: hwb) and that became disassociated from the dorsal part of the metanotum (Fig. 84: no<sub>3</sub>) when the metapleuron and metanotum (Fig. 84: pl<sub>3</sub>, no<sub>3</sub>) fused together. We are less certain of the origin of the suprapleural sensillum (Figs 85, 98: sps), but it too likely is metanotal.

In *Zealaromma*, the propodeal spiracle is posterior to the anterior margin of the propodeum (Figs 105, 109: sp) and in *Z. valentinei* the dorsal margin of the metapleuron forms a more or less evenly convex arc (Fig. 105: pl<sub>3</sub>). These features are more similar to the structure of *Mymaromella* (Figs 98, 100, 102) than *Mymaromma* (Figs 82, 84). Otherwise, the two species of *Zealaromma* have structures of the metathoracic-propodeal complex that differ from each other and from the other two genera. *Zealaromma insulare* has the metanotum (Fig. 109: no<sub>3</sub>) fused laterally with both the metapleuron and propodeum so that smooth cuticle completely separates the spiracular aperture from the anterior

margin of the composite structure (Fig. 109), whereas sutures separate the metanotum from both the metapleuron and propodeum in *Z. valentinei* (Figs 105: no<sub>3</sub>, pl<sub>3</sub>, pro; 106). In *Z. valentinei*, the posterior margin of the metapleuron is carinate dorsal to the propodeal spiracle and it overlies a smooth band that extends from the spiracular aperture to the intersection of the metapleuron, metanotum and propodeum (Fig. 105). The linear smooth region is similar to the spiracular peritreme in *Mymaromma* and *Mymaromella* except that the region is sclerotized. Although the metathoracic-propodeal structures appear to be quite different in *Z. insulare* (Figs 105, 106) and *Z. valentinei* (Figs 109, 110), in both species the postalar sensillum is widely separated from the prespiracular sensilla (cf. Figs 105, 110: pas, pss). This shared feature suggests that the metathoracic-propodeal structure of *Z. insulare* evolved from a *Z. valentinei*-like structure through fusion of the metanotum, metapleuron and propodeum. It also suggests that what appears as a laterally truncate, independent metanotum in *Z. valentinei* (Fig. 105: no<sub>3</sub>) is not structurally homologous with the laterally truncate, independent metanotum of other Hymenoptera (cf. Figs 11, 12 with Fig. 105). This conclusion is based on our hypothesis that the postalar sensillum is of metanotal origin and our observation that the sensillum sometimes appears to be disassociated from the metanotum/propodeum in *Mymaromella* because of elongation and narrowing of the anterolateral corner of the metanotum/propodeum. This transformation series is illustrated by Figs 98 → 100 → 102, and we suggest that the anterior position of the postalar sensillum in *Zealaromma* evolved through a similar transformation series. If so, the superficially laterally truncate margins of the metanotum of *Z. valentinei* are not the "true" margins of the metanotum. Dissections of *Z. valentinei* are necessary to determine whether the postalar sensillum is actually

separated from the “metanotum” or whether the apparently laterally truncate metanotum (Figs 105, 106) extends anteriorly as a slender band beneath the dorsal margin of the metapleuron and bears the postalar sensillum at its apex.

Although the structure of the metathoracic-propodeal complex of *Z. valentinei* may not be directly ancestral to the structures that characterize *Mymaromma* or *Mymaromella*, both of the latter structures likely evolved from a mymarommatid that had an independent metanotum. The structures characteristic of *Mymaromma* and *Mymaromella* could both be derived from such a hypothetical structure. Fusion of the lateral margin of an independent metanotum with the dorsal margin of the metapleuron in one lineage would result in the structure characteristic of *Mymaromma* (cf. Figs 105, 84), whereas fusion of the posterolateral margin of an independent metapleuron with the propodeum in another lineage would result in the structure characteristic of *Mymaromella* (cf. Figs 105, 98). As noted below, at least some Cretaceous representatives appear to have a propodeal spiracle in the same approximate position as in *Mymaromella* and a line extending dorsally from the spiracle (Fig. 187: sp), but it is uncertain whether this line represents a peritreme or only a smooth band. Furthermore, the presence or absence of an independent metanotum could not be determined from the amber inclusions. Both *Mymaromma* and *Mymaromella* possess a slit-like spiracular peritreme (Figs 80, 82, 84, 97–102), which is not present in *Zealaromma* (Figs 105, 109). This suggests that the common ancestor of extant mymarommatids had both an independent metanotum and a slit-like spiracular peritreme, but that the peritreme was lost in the common ancestor of *Z. valentinei* + *Z. insulare*.

We only observed a single seta dorsally between the meso-/metapleuron and scutellar-axillar complex anterior to the postalar sensillum in *Z. insulare* and *Z. valenti-*

*nei* (Figs 105, 110: dms?). Because this seta is very close to the base of the hind wing and is quite obvious we tentatively consider it as homologous with the seta on the dorsal margin of the metapleuron rather than with the suprapleural sensillum of *Mymaromma* and *Mymaromella*. However, dirt or position of wings prevented observation of the presence or absence of the different sensilla in many specimens and further study is necessary to document their distribution accurately in all species of *Mymaromma* and *Mymaromella*.

Another feature of the metathoracic-propodeal complex that differs among mymarommatids is the presence or absence a metapleural pit, and its position when present. We did not observe a metapleural pit in species of *Zealaromma* (Figs 103, 108), whereas species of *Mymaromma* have quite a distinct pit that is comparatively close to the propodeal spiracle (Figs 80–83: pl<sub>3</sub>p). Species of *Mymaromella* are variable in presence or absence of a metapleural pit (cf. Figs 95–97, 99, 101) and it is so small that often it is visible only with SEM (Figs 97, 101). Therefore, the apparent absence of a metapleural pit in some species of *Mymaromella* may be because of the angle of view or dirt concealing the minute hole. When visible, the pit is at least midway between the propodeal spiracle and the ventral margin of the metapleuron (Figs 97, 101). We are uncertain of the presence or absence and relative position of a metapleural pit in fossil mymarommatids because of the difficulty in observing such a tiny feature. However, *P. agapa* appears to have an unusually large and distinct metapleural pit that is quite close to the propodeal spiracle (Fig. 187: pl<sub>3</sub>p, sp). A few species of *Mymaromma* also have a tiny pit on the mesopleuron (Fig. 87: pl<sub>2</sub>p) at a similar height as the larger metapleural pit (Fig. 87: pl<sub>3</sub>p), but this requires clean specimens and SEM for observation.

The final variable feature of the propodeum is its structure posteriorly. In *My-*

*maromma*, the posterior margin extends as a  $\cap$ -like flange over (Figs 78, 79) and on either side of the petiolar insertion (Figs 81, 83). The flange normally conceals the propodeal foramen in dorsal (Figs 78, 79) or lateral (Fig. 80) view. If the metasoma is dissected from the mesosoma (Figs 86, 87) the propodeal foramen is seen to project slightly as a circular ring (sometimes also visible if mesosoma observed from posterolateral view, Fig. 81). The ventral edge of each side of the propodeal flange abuts the posterodorsal margin of the slightly protruding metacoxal foramen so that the two form a rigid pincer-like structure around a deep pit (Figs 80, 86: isp; 81, 83, 87). Although the posterior propodeal structures of *Mymaromma* and *Zealaromma* are superficially quite different from that of *Mymaromma*, they differ only by lacking the propodeal flange dorsally above the petiolar insertion. Consequently, the protuberant, somewhat tubular propodeal foramen is more readily visible (Figs 90–97, 99, 101, 103, 104, 107). We could not determine the exact structure of the propodeum in fossils, but they appear to have structures (Figs 184, 191) similar to those *Mymaromma* that lack a distinct vertical flange on either side of the foramen (cf. Fig. 94). In *Mymaromma* and *Zealaromma*, the rim of the metacoxal foramen and the flange on either side of the propodeal foramen form the same pincer-like structure as in *Mymaromma* (cf. Figs 92, 94, 104 with Figs 81, 87: pf). Although usually less noticeable, a similar pincer-like structure is formed between the dorsal margin of the mesocoxal foramen and the anteroventral angle of the metapleuron, and sometimes between the anteroventral margin of the mesopleuron and posterolateral margin of the pronotum (Figs 80, 86: isp). The adaptive function of the pincer-like structures is unknown. In most individuals, the anteroventral projection of the metapleuron and the ventral margin of the propodeal flange appear to extend only to the outer edge of the rim of the meso- and metacoxal

foramina, respectively, mesal to an oblique trough in the rim of the coxae dorsolaterally (Fig. 87: ct). The trough likely cradles the dorsal, constricted part of the coxa (basicoxite) that inserts into its respective foramen (Figs 81, 104, 107: bc). In *Zealaromma*, the propodeal flange projects ventrally as quite a strong digitiform process (Figs 104, 107). If the metacoxa is raised, the propodeal process would articulate within a basal groove of the metacoxa on the inner side of the basicoxite (Figs 104, 107). The lateral margin of the posteriorly protruded metacoxal foramen would likewise articulate within a basal groove on the outer side of the basicoxite (Fig. 107). Consequently, the ventrally projecting propodeal process and posteriorly projecting metapleural process may help stabilise or help control movement of the metacoxa, at least in *Zealaromma*.

Extant mymaromatids have only a single seta on the propodeum near the spiracle (Figs 84: prs; 80–83, 95–103, 109). Mymaridae usually also have only a single propodeal seta (Fig. 11: prs), though there is virtually no information concerning the distribution of propodeal setae in Hymenoptera and quite likely the number of setae is at least partly correlated with body size.

**Wings:** What we described as the distal part of the forewing stalk in mymaromatids has its anterior and posterior margins curved dorsally. In Cretaceous mymaromatids (Figs 185, 194, 195, 205) and in many extant species the recurved margins form only quite a short, U-shaped gutter basal to the widened disc surface (Fig. 125). Some extant species have the margins abutting along a longer distance to form more of a complete tube (Figs 124, 131). A slightly thicker basal part of the stalk (Figs 124: stp; 167) forms a “proximal” portion that in dorsal view has a single campaniform sensillum and seta distally (Figs 125–128: cs, mc). We consider the proximal part of the forewing stalk to be composed of remnants of the wing base



and venation similar to those of Chalcidoidea (see discussion of suprafamilial relationships). We interpret the part of the anterior convex band that folds under the wing as the costal cell (Figs 127, 129: cc; 130, 132), the region between the putative costal cell and the distal seta and campaniform sensillum as the marginal vein (Figs 95, 127, 129, 185: mv; 130, 132), and the distal part of the putative marginal vein that appears bulbous or curves slightly away from the wing margin in slide preparations or in fossils as the remnant of the stigmal vein (Figs 185: stv; 194). The retinaculum is the posterior band that in ventral view is concave (Figs 127, 132: ret). A slender band that extends toward the base of the wing from the base of the putative marginal vein, which separates the costal cell from the retinaculum, we interpret as the submarginal vein (Figs 95, 127, 132, 185: smv). In slide preparations, the regions described above as the marginal and stigmal veins often appear to be filled with air (Fig. 167), which supports the hypothesis that these represent vein remnants. The length of the putative marginal vein is variable (*cf.* Figs 95, 127, 130, 132), but our survey was insufficient to determine whether length is a generic or only a specific feature. A line of "dots" are visible near the anterior margin of what we interpret as the costal cell in some slide preparations (Fig. 167). These dots are in the same position as a line of spicules on the costal cell of some species when studied with SEM (Figs 95, 130). Other species have scattered spicules on the costal cell (Figs 129, 132). A distinct line of dots on the forewing basal to the marginal vein in some Cretaceous fossils (Figs 185, 201) suggests that a straight line is the groundplan state, but our survey of extant species was insufficient to determine whether the arrangement of spicules could be informative for differentiating supraspecific taxa.

The anterior and posterior margins of the forewing are curved into a U-shaped

gutter in *Mymaromma* sp. 10 (Fig. 125). A cross-section of the forewing immediately distal to the long seta reveals a more or less S-shaped folding pattern (Fig. 126). In cross-section, the posterior band is thin and forms a deeply concave fold that comprises the retinaculum (Fig. 126: ret), whereas the anterior band is tubular and folds dorsally upon itself so as to abut the posterior band. The tubular portion appears to be subdivided into two parts by a thin septum and the larger portion is filled with some substance. If this substance is dried haemolymph and if the smaller portion that appears empty is a trachea (Fig. 126: tra?), then this further supports the contention that the anterior tubular portion is a remnant of a vein.

Members of *Mymar* have even more conspicuously pedunculate forewings (Fig. 2) than mymarommatids. The anterior margin of the forewing (Figs 4, 5: am) is curved dorsally and is folded over to its posterior margin so as to form a longitudinally divided tube distal to where the hind wing attaches to the retinaculum. The margin is folded over immediately beyond a single long seta (Figs 3, 4: mc) and there are several campaniform sensilla (Fig. 4: cs) distal to the seta, unlike the single, more basal sensillum of mymarommatids. In *Mymar*, the long seta is homologous to the distal macrochaeta of other mymarids and the campaniform sensilla likely are all that remain of a reduced stigmal vein. Consequently, the forewing of *Mymar* is quite similar to that of mymarommatids except for position of the campaniform sensilla relative to the long seta. The sensilla are positionally correct in *Mymar*, but not in mymarommatids, if they are stigmal in origin and the long seta delimits the apex of the marginal vein. The forewings of *Mymar* are additionally similar to most mymarommatids in having long marginal setae that arise from within the wing periphery (Fig. 7). In mymarommatids, the setae are inserted conspicuously within the wing periphery only in those

species with long marginal setae (Figs 113–119, 121, 163, 165, 168). The deep insertion of the marginal setae is not apparent when these are short (Figs 120, 122, 164). The functional significance of a deep insertion for the setae likely is to minimize their flexion at the wing margin when the wing is moved through the air so as to help keep the setae in the same plane as the wing surface. This would result in the disc and projecting setae together forming a larger wing “surface”. The forewings of mymarommatids are unique in having a mesh-like pattern on the disc (Figs 163–165, 195, 211) that is formed by lines of raised membrane on both the upper and lower surfaces (Fig. 123). Although the pattern is not distinct in some amber fossils (Figs 183, 205), this appears to be an artifact of preservation. The pattern likely is less distinct in amber fossils because the resin fills the depressions between the lines of raised membrane similar to using glycerine to fill small surface irregularities in amber. The mesh-like reticulations may serve to provide strength to the relatively large wing disc so that it is not deformed as it is pushed through the air. Similarly, the longitudinal folds of the disc membrane that result in a more or less corrugated forewing in many mymarommatids (Figs 113–115) may help wing rigidity. The longitudinal folding affects wing shape to some extent because the forewings usually appear more elongate-lanceolate in species with deeper folds than in species with less distinct folding (cf. Figs 113–115, 163 with Figs 116, 118, 166). Consequently, shape and relative dimensions of the forewings can be affected by method of specimen preservation, such as slide versus dry mounting.

The length and thickness of both the marginal and discal setae are quite variable among mymarommatids (cf. Figs 113–122). Species of *Mymaromella* tend to have short, spine-like discal setae (Figs 166, 168), whereas those of *Mymaromma* (Fig. 163) and *Zealaromma* (Figs 164, 165) have lon-

ger, more hair-like setae, but there is considerable variation. The forewings of all but one species of *Mymaromma* are characterized by the presence of a conspicuously long posterobasal marginal seta that is separated by several short setae from long marginal setae apically (Figs 113–115, 163). All the posterobasal marginal setae are quite long in *Mymaromma* sp. 10, but this may be correlated with its very long and conspicuous discal setae (Fig. 116). Many species of *Mymaromella* have the posterobasal setae all short (Figs 117, 120, 166), though some have quite a long posterobasal seta (Figs 118, 119) similar to species of *Mymaromma*. The forewing marginal setal pattern of *Z. insulare* (Figs 122, 164) is modified similar to *Mymaromella* sp. 20 (Fig. 121), whereas *Z. valentinei* has a forewing marginal setal pattern that is unique among extant mymarommatids. The forewing of *Z. valentinei* has three or four quite long basolateral setae basally on the posterior margin (Fig. 165), which is similar to some Cretaceous mymarommatids (Figs 188, 194). Other Cretaceous species (Fig. 195) and some Tertiary (Fig. 211) fossils have a single conspicuously long posterobasal seta, and one Tertiary species has uniformly short posterobasal setae (Figs 207–209) (see further below).

The stalk-like hind wing of mymarommatids (Figs 135, 136) terminates in a C-like structure formed from a single, curved, socketed hamulus (Fig. 135: ham) and an opposing process that appears to be a projection of the wing (Figs 134, 135: op). Consequently, the opposing process is a functional analogue, but probably not homologous with what Basibuyuk and Quicke (1997) called “modified-erect setae”. Between them, the hamulus and opposing process grasp the hind margin of the forewing. The apex of the hamulus inserts into the retinaculum (Figs 130: ret; 129, 133) and the apex of the opposing process is appressed against the dorsal surface of the wing (Figs 134: op; 133). This

functional complex is quite similar to that of *Mymar*, in which the stalk (Fig. 2) has two socketed hamuli and additional distal projections that grasp the forewing (Fig. 5) (in some species the wing continues as filament beyond the hamuli). The hind wing stalk of mymarommatids is composed of a tubular vein along the anterior margin and sometimes a slender band of membrane posteriorly (Figs 135, 136: mb), though distinct membrane usually is not evident. The stalk has long setae along its leading margin and these setae project within the retinaculum when the wings are joined (Figs 129, 130), perhaps serving to sense position of the hind wing and/or to further position the hind wing relative to the forewing. The process of the hind wing is bifurcate in most if not all species (Figs 134–136). At least some species have longitudinal striations on the dorsal surface of the posterior band of the proximal part of the forewing. The striations likely act as “tracks” along which the bifurcation of the hind wing process slides (Figs 133, 134). Furthermore, at least some species have short, distally projecting denticles on the posterior margin of the retinaculum (Fig. 132: ret) below much of the region we interpret as the marginal vein. These denticles may function as a ratchet, enabling the hamulus and hind wing to slide distally in the retinaculum when the forewing is moved downward, but impeding movement of the hamulus if it is slid along the posterior margin of the retinaculum when the forewing is moved upward. Such a ratchet structure could be used to help maintain the fore- and hind wing complex at a specific angle relative to the body for extended periods of time. It is unknown whether the forewings can be rotated for the correct movements necessary to produce lift during upward and downward arcs of the wing. It may be that mymarommatids actually do not fly, but simply use their comparatively large forewing surfaces as “kites” and are blown passively in wind currents. If the latter, the rod-like

hind wings, apparently strong coupling system between the fore- and hind wings, ratchet slide mechanism, and other modifications of the forewing discussed above may all serve to reinforce the forewing to prevent its deformation and hold it at the necessary angle so that the individual can balloon.

**Legs:** As first mentioned by Gibson (1993), extant mymarommatids have two different structures of the protibial spur or calcar *sensu* Basibuyuk and Quicke (1995). Species of *Mymaromella* (Figs 137, 139a: ca) and *Zealaromma* (Fig. 140: ca) have a comparatively long and curved, apically bifurcate calcar, whereas those of *Mymaromma* (Figs 142, 144a, 145a: ca) have a short, simple or needle-like calcar. The protibia also has a strong, socketed seta ventroapically on either side of the calcar that originates from a tube-like elevation of the cuticle (Figs 138, 140, 141a, 144a, 145a, b: ps). Because of their position and structure, under some angles of view one of these socketed setae can be mistaken for the calcar in *Mymaromma* (*cf.* Figs 142, 143, 144a: ca, ps); however, the calcar originates from a concave region that is continuous to the apex of the protibia (Figs 144a, 145b). There is also a much smaller second projection within the concave region of some species of *Mymaromma* (Fig. 145b). Extant mymarommatids lack meso- and metatibial spurs, but there are two strong, socketed setae that originate from tube-like elevations of the cuticle ventroapically on the mesotibia (Figs 139b, 141b, 144b: ps) and metatibia (Figs 139c, 141c, 144c: ps) similar to the protibia. The two ventroapical setae project beyond the apex of the respective tibiae and usually diverge distally. We refer to the two ventroapical setae on the tibiae as “pseudospurs” because they resemble the articulated spurs of parasitic Hymenoptera with true tibial spurs. Because of their size, we were unable to determine whether spur-like projections visible on the meso- and metatibiae of some fossil mymarommatids are

true spurs or pseudospurs. We suspect they are pseudospurs because there are more than two spines on the metatibiae of some fossils similar to extant mymarommatids (Figs 139c, 144c).

The only other leg feature we found to differ among mymarommatids was the presence of small “bumps” on the posterior surfaces of the femora (Figs 143–145), particularly the mesofemur (Fig. 144) of both species of *Zealaromma*. The function of the bumps and whether or not they are campaniform sensilla is unknown.

Basibuyuk et al. (2000) examined the sensilla of the orbicula of the tarsal claws of an unidentified mymarommatid species in their review of that structure in Hymenoptera. We did not attempt to extend their survey to determine whether the character states they documented for the species vary in Mymarommatidae.

**Metasoma:** Individuals of *Zealaromma* lack cerci and have four setae in a row near the posterior margin of the syntergum (Figs 153, 155). *Mymaromma* and *Mymaromella* have cerci and these usually are almost flat, subcircular and with four long setae (Figs 150: cer; 158). The number of cercal setae is reduced (Fig. 151) in some species of both genera and rarely the cercus is almost indistinguishably integrated with the tergal surface except for being somewhat concave (Fig. 152: cer). However, there is always at least one seta that is more or less obviously associated with the cercal depression on either side of two paramedial syntergal setae. In such instances, the syntergum appears to have four setae in a row (Fig. 152) rather than the two paramedial setae (Figs 150, 151, 158) that are otherwise characteristic of *Mymaromma* and *Mymaromella*. This suggests that the cerci were lost in *Zealaromma* through their fusion with the tergal surface and that the two outer syntergal setae of *Zealaromma* are homologous with cercal setae in *Mymaromma* and *Mymaromella*. Individuals of *Zealaromma* also lack metasomal spiracles (Figs 153–155), though

males of *Z. insulare* retain a seta on Mt<sub>7</sub> (Fig. 154) that in *Mymaromma* and *Mymaromella* is associated with the spiracle (Figs 149–152).

Lin (1994, fig. 3) illustrated the male genitalia of a species identified as *M. anomalum*. Triapitsyn and Berezovskiy (2006) stated that this was a misidentification of their new species, *M. ypt*, and gave another illustration of the genitalia (fig. 9) based on their specimens. Both illustrations show a posteriorly directed Y-shaped structure over a larger medial structure. The medial structure tapers posteriorly and is divided apically; anteriorly it has lateral rods that extend for a distance greater the medial rod of the Y-shaped structure. The two drawings appear quite different from our SEM microphotographs of the male genitalia of *Mymaromma* sp. 7 (Figs 158–160), but the differences likely are mostly because of the different methods used to prepare and study the genitalia (slide mounting *vs.* SEM) rather than species differences. Microscope slide preparations of the male genitalia of *M. sp. 7* and of a specimen of *M. anomalum* from Japan also show a medial Y-shaped structure (Fig. 170: voa) and two longer and stronger paramedial processes (Fig. 170: aea) similar to those in the drawings of Lin (1994) and Triapitsyn and Berezovskiy (2006). Additionally, there are a pair of very slender, obliquely angled, somewhat sinuate structures (Fig. 170: paa?) exterior to the paramedial processes, which extend to the same level as the medial rod of the Y-shaped structure (Fig. 170). A photograph of the apex of the male metasoma of a male of *M. ypt* sent to us by Serguei Triapitsyn (UCRC) shows that it also has the slender oblique structures. The oblique structures extend anteriorly to the same level as in Fig. 170, but posteriorly they appear to articulate with the anteriorly directed arms associated with the sclerotized  $\cap$ -shaped structure (Fig. 170: syn?).

*Zealaromma* males differ conspicuously from those of *Mymaromma* and *Mymarom-*

*mella* because they have elongate-digitiform processes that project laterally from between the syntergum and hypopygium (Figs 154, 156: par). Each process has a long terminal seta and the processes point in different directions in some specimens (*cf.* inserts in Figs 155, 156), which indicates they are articulated or membranous basally. The processes resemble the exerted cerci of some Chalcidoidea (e.g. Torymidae), but there are several setae on the cerci of chalcids whether these are exerted or plate-like, similar to mymarommatids (Figs 150, 158) and some other parasitic Hymenoptera (Fig. 157). We consider the elongate processes of the male genitalia of *Zealaromma* to be parameres. The genitalic structure of *Zealaromma* is similar to that of male Maamingidae, which was described and illustrated by Early et al. (2001, figs 12, 13). The genital complex of *Maaminga rangi* Early et al. (2001) apparently lacks a phallobase, but has a medial, apically divided aedeagus (Fig. 157: aed), a volsella with a spined digitus (Fig. 157: vol, dig) ventrolaterally on either side of the aedeagus, and a digitiform paramere with two terminal setae (Fig. 157: par). The digitiform parameres of *M. rangi* widen anteriorly and articulate with the aedeagal-volsellar complex basally (Fig. 157). In microscope-slide preparations of the male genitalia of *Z. valentinei*, the bases of the externally visible parameres (Fig. 169: par) appear to be continuous with slender rods (Fig. 169: paa) that extend anteriorly lateral to the much stronger paramedial rods (Fig. 169: aea). The slender rods curve toward the aedeagal-volsellar complex at a level near the end of the medial Y-shaped structure (Fig. 169: voa), where they possibly articulate with the complex. Except for the externally projecting parameres, structure of the genitalia observed in the slide preparation of *Z. valentinei* is quite similar to that of *Mymaromma* sp. 7 (*cf.* Figs 169, 170).

The aedeagus of male chalcids has paired aedeagal apodemes (Gibson 1997,

fig. 7). We therefore interpret the longer paramedial rods visible in slide preparations of the male genitalia of *Zealaromma* and *Mymaromma* as the apodemes of the aedeagus (Figs 169, 170: aea). A pit in each smaller anterior lobe of the aedeagus (visible with SEM) may represent the base of the respective apodeme. The medial rod of the Y-shaped process in males of both genera (Figs 169, 170: voa) appears to be continuous with the two ventrolateral volsellae/digitae (Figs 161, 162, 169: dig). In the slide of *Z. valentinei*, the medial rod appears to consist of two appressed apodemes rather than just a single apodeme (Fig. 169) (also suggested in Lin 1994, fig. 3). Based on positional similarity, we suggest that the internal, obliquely angled, slender rods of male *Mymaromma* (Fig. 170: paa?) may be homologous with the internal rod-like portions of the parameres of male *Zealaromma* (Fig. 169: paa). We are uncertain as to the structural homologues of the two darker, c-shaped regions in Fig. 170. The smaller, apical c-shaped region (Fig. 170: anp?) may be a sclerotized anal plate, which separates the anus from the genital complex (Fig. 159: an, anp). The lateral longitudinal processes associated with the larger c-shaped structure appear to be lateral, anteriorly extended portions of the syntergum (Fig. 170: syn?). The larger c-shaped structure consists of lateral, slightly convex bands and a straight, transverse ventral band (Fig. 170). The former may simply be the edges of one of the tergites and the latter the edge of a sternite, but further study is necessary to resolve this.

## EXTINCT FAUNA

*Tertiary taxa.*—The only mymarommatid genus described from Tertiary amber is *Palaeomymar* Meunier. The type species, *P. succini* Meunier (1901), was based on 5 of the original 13 males and 3 females that Duisburg (1868) discussed and illustrated. We did not locate any amber inclusion we consider as part of their material (see

“Neotype designation” under *Palaeomyrmar*) and therefore base our interpretation of *P. succini* on their descriptions and illustrations.

Although Duisburg (1868) did not describe his specimens in detail he stated why he thought they probably belonged to *Mymar* Curtis. The diagnosis he gave for *Mymar* included 13-segmented antennae for males, 9-segmented antennae for females, and 4-segmented tarsi. He said that the fossils differed from *Mymar* primarily in wing features and stated specifically that the long marginal setae began near the apical half of the forewing, as he illustrated (Duisburg 1868, fig. II). The forewing of *P. succini* illustrated by Meunier (1901, fig. 12) also shows the marginal setae along the posterior margin gradually increasing in length apically, i.e., without a conspicuously long basal seta. Meunier (1901) described five rather than four tarsal segments for *P. succini*, but this discrepancy is not surprising because Duisburg (1868, fig. II) illustrated, and thus likely examined, a female at only 85x magnification. All known mymarommatids have five tarsal segments. Meunier (1901, fig. 13) only described and illustrated the 13-segmented antenna of a male and provided no information to confirm or contradict Duisburg’s comparison of the female antenna with that of *Mymar*. The habitus line drawing of Duisburg (1868, fig. II) appears to show only five funicular segments, but known female mymarommatids have either six or seven segments. Based on the stated similarity of the antenna to *Mymar*, the flagellum likely consisted of six funicular segments and an unsegmented clava.

We examined 10 Baltic amber mymarommatid inclusions, 8 from ZMUC, 1 from GZG, and 1 from NHRS. The inclusions from ZMUC contained five males and three females that likely constitute three species. The first species, represented by a male (ZMUC: 17-5/1963) and a female (ZMUC: 1-5/1967), is characterized by a long, curved protibial calcar (Fig. 212)

and a forewing that has the posterobasal marginal seta obviously longer than several setae distal to it (Fig. 211). The female also has seven funicular segments and an unsegmented clava. Based only on these features it is likely that the species, if extant, would be assigned to *Mymaromella*. Two pieces of amber, both labelled as ZMUC: 16-1/961, each has a single male. One is insufficiently preserved to determine its relevant features, but the other male has a long posterobasal marginal seta and lacks a long calcar. If extant, this male probably would be assigned to *Mymaromma*. Another two males (ZMUC: 8-19/1954, 1890-108) and two females (ZMUC: 28-3/1958, 16-1/1961) are characterized by the absence of a long protibial calcar, uniformly short setae along the posterior margin of the forewing basally (Figs 207–209), and a 6-segmented funicle in the females (Fig. 179). Because of these features we believe that this third species is the one that Duisburg (1868) illustrated and Meunier (1901) named as *P. succini*. Although Duisburg (1868) and Meunier (1901) described and Meunier (1901, fig. 13) illustrated a 13-segmented male antenna for *P. succini*, males may only have 12 antennal segments. The left antenna of the male in ZMUC: 8-19/1954 is clearly visible in ventral view. The apical four segments are all about the same length and form a differentiated clava because they are slightly thicker and more broadly attached than 6 more slender funicular segments (cf. Fig. 177). The apical flagellar segment illustrated by Meunier (1901, fig. 13) is very short and it may only be a subsection of the apical segment that is differentiated by a whorl of projecting setae. The ZMUC: 8-19/1954 male in ventral view also appears to have the propleura fused into a carapace, the mandibles lack any distinct dorsal tooth or angle, and although the labiomaxillary complex is quite broad the labium appears to be only about as wide as the maxilla. The genitalia project ventrally from the metasoma and

lateral digitiform processes (parameres) are not evident. If our observations are correct, the ZMUC amber inclusions indicate that Tertiary mymarommatids had more diverse combinations of features than the extant fauna. No extant mymarommatid has a short calcar (characteristic of *Mymaromma*) and all the setae along the posterior margin of the forewing short basally (characteristic of many *Mymaromella* but not *Mymaromma*).

The GZG specimen is a male positioned dorsal side up in a thin piece of amber glued to a microscope slide. It has a long, curved protibial calcar and the left forewing, viewed with the compound microscope, appears to have a very long posterobasal seta. Also visible are the dorsolongitudinal and dorsoventral flight muscles plus the mesotergal-trochanteral muscles. Using a compound microscope, the mesotergal-trochanteral muscle of one side clearly attaches to the apex of an obliquely projecting, rod-like axillar phragma (cf. Vilhelmsen and Krogmann 2006, fig. 13). The NHRS specimen, also a male in an amber block glued to a microscope slide, is positioned in a somewhat dorsolateral view. It also appears to have a long, curved calcar, but the forewing marginal setal pattern is not clear because the forewings are crossed over basally.

The only other described Tertiary mymarommatid, *P. duerrenfeldi*, is based on a single male from Sicilian amber. Sicilian amber is dated at about 5 mya compared to Baltic amber at about 44 mya (Grimaldi and Engel 2005). The lateral habitus drawing of *P. duerrenfeldi* provided by Schlüter and Kohring (1990, fig. 1) illustrated a comparatively long and straight (needle-like) protibial calcar and a broad forewing that is evenly rounded apically. Our study of the holotype confirmed that the calcar is long but that it is also curved distally. The forewings are most similar to those of extant *Mymaromella* because of their shape and the presence of short, spine-like discal setae (represented by dots in fig. 1 of

Schlüter and Kohring, 1990). The left wing, examined with a compound microscope, appears to have a posterobasal marginal seta that is obviously longer than several more distal short setae, though it is shorter than the posterobasal seta in Fig. 118 (the right wing also has a "line" apparently projecting from its posterobasal margin that superficially appears as a seta, but it is longer than that of the left wing and may be an artifact). The mandibles definitely are bidentate, similar to those of extant *Mymaromella* and *Zealaromma* (cf. Figs 47, 54), and the vertex appears to have ocelli under some angles of light when examined with a dissecting microscope. The body cuticle is translucent in lateral view so that presence or absence of a suture between the meso- and metapleuron is not evident. The exact structure of the propodeum cannot be determined, but it apparently does not have a strong propodeal flange because the basal constriction of the first petiolar segment is visible in lateral view (cf. Fig. 99). Schlüter and Kohring (1990, figs 1, 2) described and illustrated a 12-segmented antenna for *P. duerrenfeldi*, including seven funicular and three claval segments. The terminal claval segment of the right antenna was drawn with its basal half bulbous and its apical half more narrowly digitiform. The clava is more distinctly 4-segmented when examined with a compound microscope because a transverse line (suture) divides the two subsections of the terminal segment (cf. Fig. 177). Because the flagellum has seven distinct funicular segments we believe the antennae to be 13-segmented with a 4-segmented clava. Consequently, the female of *P. duerrenfeldi* probably has 7 funicular segments and a 1-segmented clava.

*Cretaceous taxa.*—We examined type material of all the described Cretaceous species except for *P. japonicum* Fursov et al. (2002). The unique female of *P. agapa* differs from females of other described mymarommatid species in several respects. Most conspicuously, it lacks the



highly derived head structure that characterizes other mymarommatids. The vertex, genae and temples appear to be uniformly sclerotized and finely, transversely strigose (Fig. 186). The sculpture is similar to that of the cheeks of some extant members (Figs 13, 16, 30). The vertex lacks a hyperoccipital band of pleated membrane and the convex vertex merges smoothly into the posterior surface of the head (Figs 183, 186), which is medially concave and with the occipital foramen near its center (Fig. 186). The head structure of *Galloromma bezonmaensis* is uncertain (see below), but our study of type material and/or published illustrations indicate that all other described Cretaceous species had the same derived head structure as extant mymarommatids (Fig. 198; Kozlov and Rasnitsyn 1979, figs 8, 9; Fursov et al. 2002, fig. 1).

As noted by Kozlov and Rasnitsyn (1979), the female of *P. agapa* also has a different mandibular structure than other mymarommatids. Although closed in the holotype, in lateral view the mandibles are comparatively thin and the outer surface is convex. The apex of the right mandible broadly overlaps the left mandible almost to its base and each mandible appears to be tapered to a point. Because they are closed, any internal dentition is not visible. There is a distinct transverse region between the dorsal surface of the mandibles and the oral margin, but we could not determine whether there is a labrum within this apparent "cavity". Extant mymarommatids are characterized by exodont mandibles. Each has a comparatively broad outer surface with the apex outcurved and with two or three externally visible, asymmetrical teeth. Furthermore, when closed, the apices of the mandibles do not overlap and their dorsal margins abut or even overlap the oral margin of the head capsule (Figs 18, 19; 25–31, 33–39, 47–49, 52, 54). The mandibles are not clearly visible in most fossils, but they are fully open and obviously exodont in the holotype of *P.*

*mandibulatus* (Figs 197, 198). The left mandible is completely exposed and has a blunt subapical ventral tooth and a much smaller subbasal tooth (Fig. 198: sbt). Except for the tiny subbasal tooth, the exposed mandible of *P. mandibulatus* is quite similar to that described for *Mymaromma* and *Zealaromma*. The holotype (PIN: 3311/450) and a paratype (PIN: 3311/448) of *P. senonicus* that we examined have the mandibles closed, but their apices are widely separated and we agree with the description of Kozlov and Rasnitsyn (1979) that the apex of the mandibles are bent outwards slightly. Both specimens appear to have the labium separate from the maxillae (Fig. 203), but we were unable to distinguish palpi. Bidentate mandibles that are widely separated from each other and that do not meet in the middle was also given as a generic feature of *Archaeoromma* by Yoshimoto (1975), which we confirm for *A. minutissimum* and *A. nearcticum*. The mandibles of *P. japonicum* were described as having two sharp teeth, which almost certainly are exodont based on Fursov et al. (2002, fig. 1). The exact structure of the mandibles of *G. bezonmaensis* is unknown.

The female of *P. agapa* and extant mymarommatids also appear to differ in relative position of the toruli. In *P. agapa*, when the head is viewed in profile the toruli are near the center of the head and its large eyes (Kozlov and Rasnitsyn 1979, fig. 10). In extant mymarommatids the toruli are near the dorsal margin of the eyes, regardless of whether these are reduced in size (Fig. 47) or are as large (Figs 25, 33) as those of *P. agapa* (Fig. 186). The holotypes of *P. mandibulatus* and *P. senonicus* are similar to that of *P. agapa* because they have large eyes (Figs 198, 203) and the toruli appear to originate at about mid height when the head is viewed from the left side. However, the apparent placement of the toruli can be affected by the angle of viewing in amber inclusions, as discussed below.

In addition to the cephalic differences, the holotype female of *P. agapa* has a distinctly 13-segmented antenna. When the specimen is viewed from its left side (Fig. 183), the left flagellum is in profile; the right antenna is partly concealed by the head but the apical three claval segments are exposed in dorsal view. The left antenna has seven slender funicular segments and four much wider segments that form a comparatively loosely associated clava (Fig. 180: cl; Kozlov and Rasnitsyn 1979, fig. 10). The exposed claval segments of the right antenna each have a pair of quite long and robust sensilla, one above the other, projecting from the outer surface. Each of the sensilla appear to be strongly bent basally and originate near the middle of the respective segment (Fig. 181a). The claval sensilla on the outer surface of the left antenna are not as distinct because of the angle of view, but at least the penultimate segment has two sensilla that originate near its middle, one almost at the dorsal margin and one midway between the midline and ventral margin (Fig. 181b). Because of their length these sensilla resemble s2-type sensilla of extant mymarommatids, but one or both could be unusually long s4-type sensilla. The claval segments of the left antenna also have several very short sensilla along the ventral margin (Fig. 181b) that are similar to s3-type sensilla of extant mymarommatids (cf. Fig. 72).

Females of other described mymarommatids have a clava composed of 1–4 segments, but if the clava is 3- or 4-segmented then the segments are much more compacted than in *P. agapa*. The clava is more tube-like with at least the third and fourth segments separated only by quite an obscure transverse suture (Figs 192, 196, 200, 204). Kozlov and Rasnitsyn (1979) described the female flagellum of *P. senonius* as having seven funicular and three claval segments, and they illustrated (fig. 8) a paratype in dorsal view with three claval segments. Our study of this

paratype in ventral view at 200x magnification revealed two distinct basal claval segments and a terminal segment that is nearly as long as the combined length of the two basal segments (Fig. 204). At 400x magnification the terminal segment also appears to be subdivided by a transverse suture, suggesting four claval segments (one or two very fine transverse lines also appear to subdivide the “fourth” segment). On one side of the clava is a strong, basally bent sensillum that extends from the apex of each of the two basal claval segments and from the “third” segment at the apparent suture line. The apical “fourth” segment has an additional three strong sensilla on the same side. The other side of the clava also appears to have strong sensilla, but they are less distinct and we are uncertain of their number and position. Kozlov and Rasnitsyn (1979, fig. 9) illustrated and described a 4-segmented clava for the holotype female of *P. mandibulatus*. Our study of the holotype in ventral view shows that the right antenna has seven funicular segments and only three distinct, coalesced claval segments (Figs 199, 200), though possibly there is a small and very poorly differentiated terminal segment. Seta-like sensilla are visible projecting from the claval segments (Fig. 200), but not clearly enough to be confident of their number.

Yoshimoto (1975) stated that females of *Archaeromma* have seven funicular and four claval segments. Females identified as either *A. minutissimum* or *A. nearcticum* in the CNC have a distinct clava because it is longer and slightly thicker than any funicular segment, but the claval segments are strongly compacted. Consequently, the sutures and the number of segments comprising the clava are indefinite. At least three claval segments are visible for some females. The female in CNC: CAS-1113 has distinct sutures differentiating two basal claval segments and a terminal part that forms about half the length of the clava. This specimen and the female in CNC: CAS-119 also has other fine,

transverse lines on the terminal claval "segment" that suggest possible additional segmentation. The basal two claval segments of CAS-1113 each have two long, basally bent sensilla on one side; there are other long sensilla on the terminal part but we are uncertain of their exact number. The female in CNC: CAS-343 has six long, basally bent sensilla on one side of its compact clava, whereas other females usually have variably long, basally curved sensilla on one or both sides. Yoshimoto (1975) also described *Protooctonus masneri* as having seven funicular and four claval segments. Our study of the holotype revealed that the compact clava has only three distinct segments (Fig. 196). Although the clava appears to have more or less uniformly long seta-like sensilla in some angles of view (Fig. 196), in other angles the sensilla are longer on one side than the other.

The specimen that Kozlov and Rasnitsyn (1979) described as the male of *P. agapa* differs in several respects from the female. The most significant difference is that the posterior surface of the head is collapsed within the head capsule in a manner similar to extant mymaromatids having the occipital plate rotated anteriorly. The similarity includes a  $\cap$ -shaped occipital margin and a comparatively wide, infolded ventral margin that together form an abruptly margined, acute angle laterally. Furthermore, the occipital foramen appears to be at the ventral margin of the head. The mandibles, although slender relative to those of extant mymaromatids, also appear to have the exterior surface slightly outcurved apically, or at least the exterior surface is somewhat concave medially. The two mandibles are angled toward each other such that their apices extend slightly beyond the oral margin and almost meet medially. The left mandible, visible in lateral view, is expanded ventrally and is differentiated into a small, acutely angled submedial tooth and a longer, slender, apical tooth, as was

described and illustrated by Kozlov and Rasnitsyn (1979, fig. 11). The antennae are 13-segmented and typical for male mymaromatoids, i.e., filiform with all the flagellar segments having a whorl of long setae medially to subapically. The apical four antennal segments, particularly the apical two, are slightly more strongly coalesced to form an inconspicuously differentiated clava. Kozlov and Rasnitsyn (1979) also noted that the eyes are somewhat larger and the first petiole segment markedly shorter in the male than in the female; furthermore, the ocelli are unusually large. Although described from the same amber deposit, the differences between the unique female and male of *P. agapa* suggest that they could represent the opposite sexes of two different taxa.

Species described in *Archaeomma* and *Protooctonus* are about 75 mya, whereas *Palaeomyrmar senonicus*, *P. mandibulatus* and *P. japonicum* are about 85 mya and *P. agapa* is about 95 mya. Only *Galloromma bezonnaisensis*, described from amber dated at about 100 mya, is older than *P. agapa* (Table 1). The unique holotype of *G. bezonnaisensis* is in a slender shard of amber that is double embedded in clear epoxy resin. The first resin block was ground to within 0.2 mm of the shard surface (Schlüter 1978) in which the dorsal surface of the specimen and the antennae face up, and then was re-embedded so that the specimen is now encased in a comparatively large block (12 × 12 × 10 mm) of resin. Visibility of the specimen in dorsal view is similar to that shown in the illustrations provided by Schlüter (1978, fig. 50; plate 5, fig. 3; plate 11, fig. 2), though in dorsal view artifacts largely conceal all but the two antennae and the right forewing (Figs 214, 216). In lateral view, a visible boundary line between the two resins is so close to the fossil that it prevents observation of the specimen with the same clarity as photographed by Schlüter (1978, plate 5, fig. 2). The latter photograph is reproduced here as Fig. 215.

The habitus drawings given with the original description of *G. bezonnaisensis* illustrate a comparatively thin mandible that is acutely tapered both in lateral (Schlüter 1978, fig. 49) and dorsal (Schlüter 1978, fig. 50) views. In dorsal view, the presumed left mandible (Fig. 217: mnd) projects anteriorly from near the lateral margin of the head capsule. It is comparatively short and evenly tapered to a point, i.e., neither obviously exodont nor curved mesally. Because of its position and length, the apices of the two mandibles presumably would not meet if they were closed. However, the head is not clearly visible (Fig. 217) and it is possible that only the tip of the mandible is exposed (cf. Fig. 193). We cannot confirm the structure of the mandible drawn in lateral view by Schlüter (1978, fig. 50), but in the photograph (Fig. 215) it appears to be similar to the mandible *P. agapa*. The photograph (Fig. 215) and lateral habitus drawing in Schlüter (1978) also show a high-triangular head that dorsally is acutely angled. What appears to be the posterior surface is obliquely angled and almost straight, and therefore could be a flat or collapsed occipital surface that is acutely angled relative to a more obviously convex frontal surface. However, if the "posterior" surface is a flat or collapsed occipital plate then the antennal toruli are almost contiguous with the posterior limit of the vertex (Fig. 215), which is unknown for any other mymarommatid. Such a high placement of the toruli would also suggest the absence of ocelli, which all other Cretaceous mymarommatids apparently have. Based on our study of other amber inclusions (see below) we suspect that the high-triangular head is partly an artifact of preservation and the angle of view, and that both the anterior and apparent "posterior" surfaces comprise the face. If so, the antennal toruli are near the center of the head, similar to *P. agapa* and at least some other Cretaceous mymarommatids. The habitus line illustrations in Schlüter (1978, figs 49, 50) do not

help resolve this problem. In lateral view, the antennae appear to be inserted near the middle of the eyes as in *P. agapa*, whereas in dorsal view they appear to be inserted at the dorsal margin of the eyes as in mymarommatids with a differentiated occipital plate. Different interpretations can also be given for the comparatively long ventral surface of the head anterior to the mesosoma (Schlüter 1978, plate 5, fig. 2). If the "posterior" surface of the head is a flat or sunken occipital surface then the position of the mesosoma indicates that the occipital foramen is near the ventral margin of this region, similar to extant mymarommatids. However, based on the lateral habitus photograph in Schlüter (1978), and our own observations, the mesosoma appears to attach to the head from under the "ventral" surface (Fig. 215). If so, this supports an hypothesis that both the apparent anterior and "posterior" surfaces constitute the face, and that the head is not structured as for extant mymarommatids. The sex of the specimen was not stated and is ambiguous based on antennal structure. Schlüter (1978) described the antenna as being 14-segmented with 8 funicular and 4 claval segments. Our study shows that there are four distinct, broadly appressed claval segments that are separated by oblique sutures (Fig. 214), but only seven funicular segments (Figs 214, 216). The claval structure indicates a female antenna. Furthermore, male mymarommatids usually have most of the flagellar segments of similar length and/or these widened medially because of the characteristic medial whorl of setae (cf. Figs 171, 172 and Figs 176, 175), whereas at least the basal four segments of the left flagellum of the holotype of *G. bezonnaisensis* are comparatively short and uniformly widened distally (Figs 214, 216). However, the terminal segment of the flagellum appears to be smaller than the penultimate segment (Schlüter 1978, fig. 50) and, as noted by Schlüter (1978), the flagellar segments have quite long and conspicuous setae

(Fig. 216: fs). These last two features are more characteristic of a typical male flagellum than that of a female, though some Cretaceous amber fossil females have quite distinct setae (Figs 196, 204). The illustrations of the antennae in lateral view given in Schlüter (1978, fig. 49; plate 5, fig. 2; plate 11, fig. 1) show a much more distinctly filiform flagellum (Fig. 215), which is also characteristic of a male antenna. However, the flagellum likely appears filiform in lateral view (Fig. 215) because the claval segments are compressed rather than cylindrical in cross-section. Consequently, their perceived width depends on the angle of view (Fig. 214; cf. Figs 181a, 181b). A short, dark region projecting posteriorly from the gaster could be the apex of ovipositor sheaths (Fig. 215: ovs?), but because of the condition of the specimen this cannot be confirmed. Furthermore, the gaster appears to be oval in cross-section (Fig. 215). Although gastral shape is not diagnostic, males usually have the gaster flattened whereas females more commonly have it oval in cross-section. The first petiolar segment is only slightly longer than the second segment in lateral view (Fig. 215) and therefore is very similar to the structure of *P. agapa* (Fig. 184), though petiolar structure does not seem to be sexually dimorphic or a generic feature (see further below). Finally, the setae along the posterobasal margin of the forewing are all quite long and of a similar length (Fig. 216).

In addition to the described taxa discussed above, we studied undescribed mymarommatooids from GPPC and AMNH Burmese amber. Burmese amber is dated at about 95–105 mya (Grimaldi and Engel 2005) and therefore the fossils are at least as old as *P. agapa* and *G. bezonnaisensis*. The GPPC material consisted of four inclusions containing three females and one male. The best preserved female (GPPC: HY17A) is in a clear piece of amber and is visible in both dorsal and ventral view, though in dorsal view a vertical crack cuts through the left

antenna at the base of the sixth funicular segment and the left half of the head and mesosoma are partly obscured. This female is similar to that of *P. agapa* because in dorsal view the vertex is transversely strigose and uniformly convex, the posterior margin of the head lacks an abrupt margin and is shallowly concave, and the temples are comparatively long (Fig. 213). In ventral view, the lower posterior surface of the head is distinctly concave between the mouthparts and occipital foramen. Although the exact structure of the labio-maxillary complex is not visible, the mandibles are open so that their apices project anteriorly, distinctly beyond the head capsule (Fig. 193). They are conspicuously curved and, based on length and the distance between their bases, it is obvious that if closed one mandible would cross over the other. Each mandible is thicker basally and strongly tapered to a slender point. Although the base of the right mandible is obscured by what appears to be head tissue, a small subbasal tooth is clearly visible on the left mandible (Fig. 193: sbt). This female also resembles *P. agapa* because it has a 13-segmented antenna with four distinct claval segments. Both antennae project obliquely in the amber block so that the segments are foreshortened in dorsal or ventral view (Fig. 182), but because of the view it is definite that the claval segments are articulated. In ventral view, the middle two segments of the clava each have one, and the apical claval segment two, long, robust, basally bent sensilla on either side (Fig. 182, black arrows). Because of the oblique view of the antenna it is difficult to be certain where on each segment the sensilla arise, though the ventral sensilla of the middle two claval segments appear to originate from the apical margin of the respective segment (Fig. 182). The basal claval segment and the apical funicular segment also have what appear to be straight sensilla projecting from the respective segments (Fig. 182, white arrows).

These may be a different type or the same type as the other sensilla, but differ in appearance because of the angle of view. The protibial calcars are curved distally and have a short inner tine subapically, and because of their length resemble the long calcars of *P. agapa* (Fig. 183, insert). The relative position of the toruli is unknown because the head cannot be observed in lateral view. We are also uncertain of the marginal setal pattern because the forewings are partly twisted over the body, but there appear to be about 15 subequally long setae along the posterior margin basal to the longer distal marginal setae. If accurate, this setal pattern differentiates the species from *P. agapa*, which has three or four (the two wings differ) comparatively long basal setae followed by several shorter setae basal to the longer distal marginal setae (Fig. 188). The forewings of *P. mandibulatus* (Fig. 202), *P. senonicus* (Fig. 205) and *P. japonicum* (Fursov et al. 2002, fig. 1) all have a single, long, posterobasal seta followed by several shorter setae. Because of preservation, the forewing marginal setal pattern was not visible for all examined Canadian Cretaceous amber specimens. Most specimens appear to have a variable number of short setae distal to a single long posterobasal seta. The holotype of *A. nearcticum* (CNC: CAS-76) has about five short setae distal to the long seta, a pattern also possessed by one female (CNC: CAS-845) and one male (CNC: CAS-748) identified as *A. minutissimum*. Another female identified as *A. minutissimum* (CNC: CAS-1160a) clearly has nine short setae distal to the long posterobasal seta. However, one female paratype of *A. nearcticum* (CNC: CAS-598) has three quite long and three shorter setae basal to the much longer distal marginal setae (Fig. 194), which is similar to the setal pattern of the *P. agapa* female (Fig. 188). Consequently, the forewing marginal setal pattern either is quite variable in Canadian Cretaceous species or the fossils represent several species. Regardless, the presence or

absence of a single long posterobasal seta likely is species-specific rather than correlated with fossil age or lineage.

A second Burmese female (GPPC: HY17B) is also in clear amber but is not visible in dorsal view because of the dimensions of the amber block and a crack above the specimen. In ventral view, the antenna has seven funicular segments and at least three claval segments that form a compact tube. The apical "segment" constitutes nearly half the length of the clava, but it might be subdivided. Projecting from along one side of the clava are four very long and thin, suberect, seta-like sensilla (one each on basal two claval segments and two on apical half of clava). At least the apical two funicular segments have similar long setae. Robust, curved sensilla are not clearly visible, but shorter, more prone setae project from the other side of the clava. The protibial calcars are curved and an inner tine is not visible. Because of this the calcar resembles one of the curved setae of the fine comb of the basal tarsal segment of extant taxa (*cf.* Fig. 137: fc). The apparent absence of an inner tine might be because of the angle of view, though a tine is not visible on either calcar using either a binocular or compound microscope. This specimen demonstrates that the angle of view can make a big difference for interpreting structure within amber inclusions. In ventral view, the head is obliquely angled with the mandibles toward the viewer. In this view, the frontal surface of the head is comparatively long and thin and the toruli appear to be very high on the head, slightly above the dorsal margin of the eyes. However, in lateral view the head is lenticular and the toruli are near the center of the face (the eyes are not evident so the position of the toruli relative to these is not known). The head is observed slightly from the posterior in lateral view. The center of the head appears to be collapsed and the dorsal and lateral posterior margins  $\cap$ -like margined. What appear to be two, apically tapered, thin

mandibles project anteriorly, though we could not determine their structure. The posterior margin of the forewing has seven comparatively short marginal setae that gradually increase in length distally. The third female (GPPC: HY17C) is clouded by sphericles within the amber block and is not clearly visible, but in dorsal view the posterior surface of the head resembles an occipital plate because it appears to be semicircular and slightly concave. The male (GPPC: HY17D) is in clear amber, but only partly visible in lateral view. In this view, the head is similar to that of the GPPC: HY17B female except that it is more highly convex and the toruli apparently are near the center of its large eyes and face. The head resembles that of *G. bezonniaensis* (Fig. 215) because the antennae originate at the widest point, though it is not nearly as acutely triangular. Two apically tapered, comparatively thin and curved mandibles project distinctly beyond the head.

We examined seven specimens in five Burmese amber inclusions from the AMNH, of which only one was a female. This female is in a block (AMNH: B-0107) of resin-embedded amber (see Grimaldi et al. 2002) together with a male. The mandibles project anteriorly, distinctly beyond the head, and their apices overlap even though they are only partly open (Fig. 189). The apex of right mandible clearly extends beyond the midline of the head (Fig. 189) and, if closed, would extend to the base of the other. In dorsal view, each mandible is tapered apically and curved toward the other (Fig. 189) and in lateral view is quite thin (Fig. 190). Only the left mandible is completely exposed and its inner margin lacks a distinct subbasal tooth, though it has a subbasal angulation because the base is broader than the tapered apical portion. The antenna is 13-segmented, including a clava composed of four broad, distinctly separated segments (Figs 189, 190). In lateral view, the first three claval segments each have one, and the apical claval

segment two, robust, basally curved sensilla along one side. The sensillum of at least the second and third claval segments originates near the middle of the respective segment, whereas the two sensilla of the apical segment are near the basal and apical third. At least the second and third claval segments have a robust sensillum on the other side projecting apically from the respective segment. The head is quite long in frontodorsal view (Fig. 189), but in lateral view it is more or less lenticular with the toruli near its center and that of its large eyes (Fig. 190). A uniformly convex vertex is not as evident as in *P. agapa*, but the vertex is rounded without any indication of an acute angle or pleated membrane. In lateral view, the posterior surface of the head appears to be concave with the occipital foramen near its center (Fig. 190). The forewings have 13 or 14 comparatively short, subequally long marginal setae along the posterior margin basally (*cf.* Fig. 191), similar to the GPPC: HY17A female. The mesosoma, in somewhat dorsolateral view, has a large circle very near the anterior margin of the propodeum that may be the spiracle, and a groove below it that extends to the posterior margin of the propodeum. We are uncertain of the exact structure of the propodeal foramen, but in lateral view the anterior (basal) flange of the first petiolar segment is clearly visible posterior to what appears to be a slightly protruding orifice (Fig. 190). The male in the same amber piece (Fig. 191) and the female of *P. agapa* (Fig. 184) have similar propodeal structures. The male is best observed from the side opposite the female, which presents a dorsolateral view of its body (Fig. 191). The posterior of the head is concave or more or less collapsed. A transverse ridge or angulation extends across the head above the occipital foramen, with the surface ventral to the ridge much more strongly concave or collapsed than the surface dorsal to it. The surface dorsal to the transverse ridge is somewhat similar to



an occipital plate of extant mymarommatids, but it is much more transverse, concave rather than flat, and lacks evident pleating or transverse ribs of sculpture. Furthermore, the front of the head immediately above the toruli is also slightly collapsed so that there is a transverse ridge between the eyes. In Chalcidoidea, a collapsed head, particularly the posterior surface of the head, is common for air-dried, weakly sclerotized specimens. The left mandible of the male is partly visible and it is similar to that of the female except for apparently having an inner tooth subbasally (Fig. 191). The presence or absence of a small inner tooth could be a sexual or taxon-specific feature or it could simply depend on the angle at which the mandible is viewed, particularly if the inner tooth or angulation projects externally, i.e., is somewhat exodont rather than flat and in the same plane as the rest of the mandible. The wings of the male are more clearly visible than for the female and the right forewing has 14 comparatively short setae along its posterior margin basally (Fig. 191). Both the female and male also have the first petiolar segment conspicuously longer than the second petiolar segment (Figs 190, 191). As for other extant and extinct mymarommatids, the male has the anterior margin of the base of the forewing folded under and there is a distinct, short marginal vein with at least one seta projecting from near its apex. The hind wing is reduced, apically bifurcate, and clasped to the forewing as described for extant members. The male also has what appears to be a large propodeal spiracle and a very long, apically bifurcate protibial calcar (Fig. 191, insert).

The forewing setal pattern and petiolar structure shared by the AMNH: B-0107 female and male suggest that they are the opposite sex of the same species and a different species than *P. agapa* and *G. bezonnaisensis*. Another Burmese male (AMNH: Bu-160) likely represents a third specimen of the species based on a very

similar forewing marginal setal pattern. Observed from its left side, the propodeum appears to have a long seta posteromesal to a large circular spiracle similar to extant members. Observed from the right side, a short line extends dorsally from the propodeal spiracle, which could be the spiracular peritreme, and forms a convex arc with the dorsal margin of the pleuron similar to the structure of *Mymaromella*. From either side, a complete metapleural suture and distinct metapleural pit are also visible. The head, seen in ventral view, is not collapsed but is distinctly concave similar to that of the *P. agapa* female. In dorsal view, the toruli are near the center of its head and large eyes and its mandibles are as described for the AMNH: B-0107 male. The metasoma also has at least four long setae projecting from its apex, but the exact number of setae and their position is uncertain because they project from somewhere under a large overhanging tergite. A third Burmese male in one of two inclusions labelled as AMNH: Bu-184, seen in dorsolateral view, has the posterior surface of the head deeply collapsed such that the temples appear very long, with parallel horizontal margins facing dorsally. The parallel margins extend anteriorly beyond a small dorsal region that has the ocelli, and extend ventrally as very thin lateral walls relative to a lower, flat, horizontal surface. The head structure is similar to mymarommatids with an occipital plate collapsed into the head except for the differentiated dorsal region bearing the ocelli and the carinate posterior margins of the frontal plate facing dorsally. If it could be viewed in profile, the head likely would have a shape similar to that of *G. bezonnaisensis* (Fig. 215). Because of the angle of view the mandibles are not visible and we are uncertain of the forewing marginal setal pattern. The specimen has a very conspicuous posterior scutellum and a distinct oval region over the base of the forewing next to the concave posterolateral margin of the mesoscutum. This structure

appears to be the same as what we interpret as the humeral plate in extant mymarommatids. Remnants of muscle tissue, including the dorsolongitudinal and dorsoventral flight muscles, are visible. A slender, vertical band of muscle tissue immediately posterior to the dorsoventral flight muscle of the right side almost certainly is the mesotergal-mesotrochanteral depressor. A separate amber block under AMNH: Bu-184 has another more poorly preserved male. This male has the posterior surface of its head conspicuously concave or collapsed and a smaller, slightly collapsed subtriangular vertical region that bears the ocelli. The concave posterior surface is reticulate ventrally, but about its dorsal half is transversely striate. The head is therefore similar to extant members with a collapsed occipital plate, though without a distinct occipital plate. Although the mandibles are not clearly visible in ventral view they do not appear to be exodont. The forewing marginal setae also are not clearly visible. A fifth male (AMNH: Bu-997) has the posterior of the head deeply collapsed behind the ocelli and the toruli apparently near the middle of the head. The forewings have seven setae along the posterior margin basally that are obviously shorter than the more distal marginal setae. These seven setae differ in length, the more basal and apical setae being longer than the medial setae. The left forewing is exceptionally well preserved. Adjacent to the body is a brownish sclerite that is acutely angled distally, which we interpret as the humeral plate. This is separated by a narrow hyaline "break" from a slender brownish band that extends distally along the leading margin of the wing. Along this brown line is a row of "dots" similar to slide preparations of some extant species (Fig. 167). Although not mentioned by Kozlov and Rasnitsyn (1979), the forewings of *P. agapa* (Fig. 185) and *P. mandibulatus* (Fig. 201) also have a row of distinct dots basally along the leading margin. In the AMNH:

Bu-997 male, the leading margin of the wing curves posteriorly distal to the row of dots so that the wing appears constricted and there is a distinct, brownish circle from which a seta projects (*cf.* Fig. 185: mc), similar to extant mymarommatids (Figs 127, 128: mc). Kozlov and Rasnitsyn (1979) stated that the tip of the forewing vein (equivalent to the brownish circle in AMNH: Bu-997) was markedly widened backwards in the *P. agapa* female (Fig. 185), and that the vein has one medial and three apical setae, of which two are short. The long distal seta in *P. agapa* (Fig. 185: mc) and the AMNH: Bu-997 male is also visible in the holotype of *P. mandibulatus* (Fig. 201) and several other amber specimens. The AMNH: Bu-997 male, *P. agapa* (Fig. 185) and *P. mandibulatus* (Fig. 201) also have a longitudinal brownish line extending proximally from the seta for nearly one-third the distance to the body, which we interpret as the submarginal vein (*cf.* Figs 95, 185: smv), and faint, almost spectral parallel lines along the posterior margin that we interpret as the retinaculum. The holotype of *P. mandibulatus* very clearly has a slender retinaculum that comprises about the posterior half of its forewing basally, and a stalk-like hind wing with a long seta basally and an apical process inserted into the retinaculum (Fig. 201). The sixth Burmese male (AMNH: Bu-479) is visible from both sides, with the head either in fronto- or posterolateral view. In frontolateral view, the toruli are within the dorsal third of the head, almost at the level of the dorsal margin of the eyes. The dorsal and lateral posterior margins of the head appear to be abrupt, though in posterolateral view the structure and the extent to which the posterior surface of the head is collapsed is not clear. Neither the mandibles nor the forewing marginal setal pattern are visible.

In addition to Burmese amber, we examined three males from New Jersey amber (about 90 mya *vide* Grimaldi and

Engel 2005). All the specimens (AMNH: NJ-179, AMNH: NJ-686a, AMNH: NJ-1005) have the posterior of the head  $\cap$ -like carinate, with the posterior surface collapsed similar to extant members with the occipital plate rotated anteriorly (Fig. 15). Two of the specimens (NJ-179, NJ-1005) have the protibial calcars visible. They are slightly curved and obviously shorter than those of the Burmese amber specimens. The left calcar of the NJ-1005 specimen has a fine inner tine originating quite far from its apex (cf. Fig. 140). Although the specimens are not well preserved, NJ-179 and NJ-686a appear to have bidentate, exodont mandibles. At least NJ-179 has ocelli, a suture separating the meso- and metapleura, and a structure of the propodeal foramen similar to that described for *P. agapa* and the Burmese amber fossils. The forewings of NJ-686a are not visible, but NJ-179 and NJ-1005 have a conspicuously long posterobasal marginal seta separated by several very short setae from long marginal setae apically (Fig. 195). Consequently, the three New Jersey Cretaceous amber specimens appear to be more similar to *P. japonicum*, *P. mandibulatus*, *P. senonicus* and at least some Canadian Cretaceous amber specimens than to most Burmese amber fossils.

Alonso et al. (2000) stated they had a male from lower Cretaceous Spanish amber (about 115 mya *vide* Grimaldi and Engel 2005) that is intermediate in structure between Mymarommatidae and Mymaridae. The specimen has a 2-segmented petiole but apparently lacks all the other features of Mymarommatidae. Among other features, they described a forewing with a submarginal vein, a small alar membrane and short marginal setae, and an 11-segmented flagellum lacking multiporous plate sensilla. Because of these features they suggested that the specimen might be considered as belonging to the sister-group of Mymaridae + Mymarommatidae. They did not illustrate the specimen and we were unable to obtain it for study.

## SYSTEMATICS

The distribution of 28 variable features that are potentially informative for establishing monophyly and relationships of supraspecific taxa in Mymarommatoidea is given in Table 2. *Mymaromma* sp. 9 is treated separately from other *Mymaromma* because it differs in several features from other examined species of the genus. *Zecalaromma insulare* and *Z. valentinei* are also treated separately because these two species differ in several features. The matrix codes and character states are described in Appendix III. State 0 designates the hypothesized plesiomorphic state for 22 of the characters (1–3, 6–11, 14–24, 26–28). Polarity decisions for these characters are based on observed states in *Galloromma* and/or other parasitic Hymenoptera. Characters 4, 5, 12, 13 and 25 represent features of extant mymarommatoidea that are too small to be observed confidently in fossils and for which other Hymenoptera cannot be used to hypothesize polarity. Our hypotheses of generic relationships and character-state evolution discussed below are illustrated by Fig. 1.

*Suprageneric classification.*—As far as can be determined, the oldest mymarommatooids that we examined had external structures of the mesosoma and metasoma similar to extant species. They also had the same highly derived forewing and hind wing structures of extant mymarommatooids (cf. Figs 129, 167 with 185, 194, 201) and likely lacked meso- and metatibial spurs, though we cannot be certain whether tibial spines visible in some fossils are pseudo-spurs or true tibial spurs. Tubular meso-tergal-trochanteral muscles originating from rod-like axillar phragmata are visible in some Tertiary and Cretaceous (Fig. 206) fossils, but our study was insufficient to evaluate other internal features that Vilhelmsen and Krogmann (2006) proposed as autapomorphies of Mymarommatoidea (propleural and profurcal arms fused, prophragma with rods, metafurca absent).

Table 2. Observed character-state distribution in Mymarommatoidae. Symbols: na = non-applicable, ? = unknown state, / = both states present. Characters and states are described in Appendix II.

Taxon	Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
Galloromma		0	0	0	?	?	0	?	?	0	0	0	?	?	0	0	?	0	0	0	?	0	0	?	?	?	?	?	?	?
Archaeromma		1	1	?	?	?	0	0	?	0/1	1	0	?	?	0	0	?	?	?	0	?	0	0/1	0	?	?	?	?	?	?
Palaeomymar		1	1	0	?	?	0	0	?	3	na	1	?	?	1	0	?	?	?	?	0	?	0	2	1	?	?	?	?	1
Mymaromella		1	1	0	1	0/1	0/1	0	0	3	na	0	0/1	1	0	0	2	0/1	1	0	0	0	0	1/2	0	0	0	0	0	1
Zealaromma insulare		1	1	0	0	0	1	0	1	2	1	0	0	0	0	1	3	1	na	0	1	0	2	0	1	0	1	1	0	0
Z. valentinei		1	1	0	0	0	0	0	1	2	1	0	0	0	0	1	0	1	na	0	1	0	0	0	0	1	0	1	1	0
Mymaromma		1	1	1	0	1	0/1	1	1	3	na	0/1	0	0	1	1	1	0	0	1	0	0	0/1	1	0	1	0	0	0	1
Mymaromma sp. 9		1	1	0	0	1	1	0	?	3	na	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	1

Contrary to Gibson et al. (1999), fusion of the propleura into a carapace (14: 1) and fusion of the mesopleuron, metapleuron and propodeum below the spiracle (15: 1, 16: 1–3) are not groundplan features. Furthermore, the holotype of *P. agapa* and some Burmese amber fossils lack the bizarre head structure, exodont mandibles, and female claval structures of extant mymarommatids. These Cretaceous fossils indicate that the mymarommatoid groundplan structure included a uniformly sclerotized head capsule (1: 0), non-exodont mandibles (2: 0), and a 13-segmented female antenna with 7 slender funicular segments and 4 wider apical segments that formed a loosely associated clava because the segments were distinctly separated (10: 0; Figs 180, 189, 190). The fossil record indicates a transformation series in which the four claval segments first became closely associated to form a compact tube (10: 1; Figs 71, 192, 196, 200, 204) prior to the apical two segments, and ultimately all the segments, fusing together to form a single claval segment in Tertiary and most extant mymarommatids. Cretaceous females that we classify in *Archaeromma* only have three distinct claval segments (Figs 196, 200, 204), but some species may have had a compact 4-segmented clava.

The cephalic, mandibular, and antennal structures of the holotype of *P. agapa* strongly support classifying this species in a separate genus that constitutes the sister group of all other mymarommatoids. The genus could simply be classified as one more genus in Mymaromatidae or because of its postulated relationships with other mymarommatids be recognized as a higher taxon equivalent to all other mymarommatids. This higher taxon could be a separate subfamily in Mymaromatidae or a family equal to Mymaromatidae. Either of the latter two classifications imply a sister-group relationship and a greater morphological “gap” between it and the other recognized genera, which would not be implicit if the genus was simply

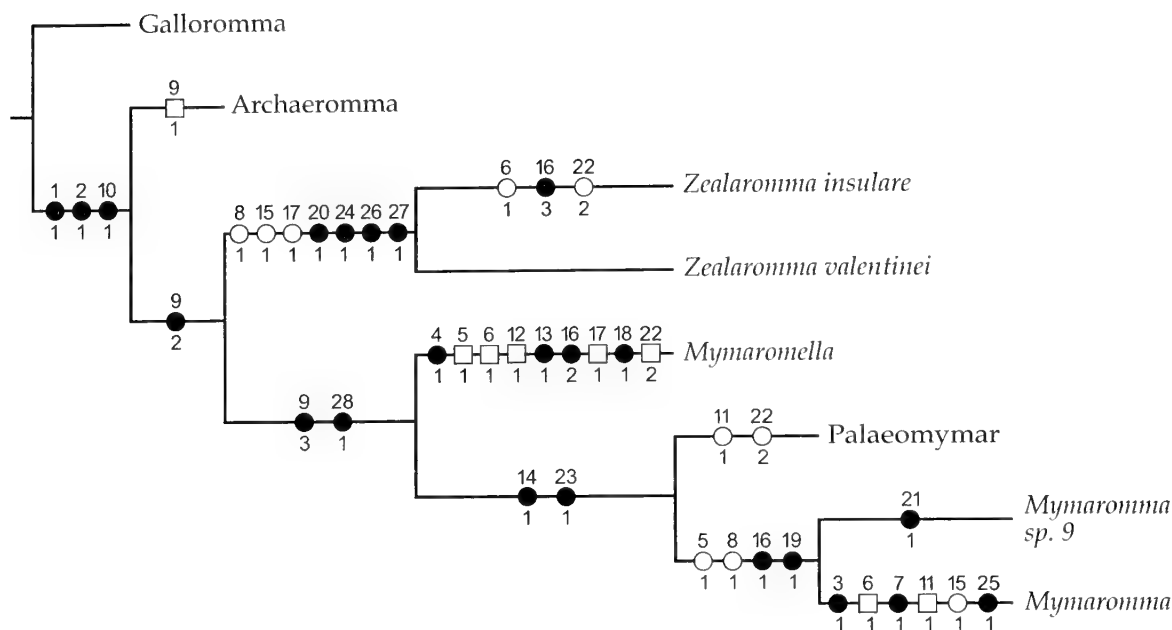


Fig. 1. Hypothesized relationships and character-state evolution among genera of Mymarommatoidea. Extant taxa in *italics*. Symbols used: ● = synapomorphic feature, ○ = homoplastic feature, □ = feature derived within taxon.

classified as one of several genera within Mymarommatidae. For these reasons, we prefer to classify the genus containing *P. agapa* separately within a higher taxon. Because the bellows-like head of mymarommatids is unique within Hymenoptera, and so bizarre, we prefer not to change the existing morphological family concept of extant Mymarommatidae. We therefore recognize two families in Mymarommatoidea, one of which is extinct. Below, we establish a new family for the genus containing *P. agapa* and, except for *G. bezonnaisensis*, classify all other described Cretaceous, Tertiary and extant mymarommatoids in Mymarommatidae. This family classification will have to be re-evaluated following study of the male from lower Cretaceous Spanish amber that was discussed by Alonso et al. (2000). If they described the features of this male accurately, then it could represent the sister taxon of Gallorommatidae + Mymarommatidae.

A remaining quandary is whether the genus containing *P. agapa* is new or congeneric with *Galloromma*. The head

structure of the unique specimen of *G. bezonnaisensis* cannot be determined. Because its head is conspicuously high-triangular (angular) in profile (Fig. 215), it seems unlikely that the vertex and temples are smoothly rounded into the occiput as in *P. agapa* unless the apparent shape is an artifact of preservation and/or the angle of view. Our study of other amber fossils shows that the angle of view can affect apparent head shape. As discussed above, the mesosoma appears to attach to the "ventral" surface of the head (Fig. 215) and, if so, indicates *G. bezonnaisensis* had a uniformly sclerotized head capsule. The structure of the single visible mandible is uncertain, but in lateral view (Fig. 215) it appears to be thin and tapered (*cf.* Fig. 190). Although the sex of the holotype is also uncertain, in dorsal view the flagellum appears to have 4 distinct claval segments (Fig. 214). The premise that the specimen is a female may be supported by the gaster not being flattened and by what might be ovipositor sheaths projecting posteriorly from the gaster (Fig. 215: ovs?). The posterior margin of the forewing

has several comparatively long setae basally (Fig. 216) similar to *P. agapa* (Fig. 188) and some undescribed Burmese amber fossils (Fig. 191) that we consider to belong to the same genus. Finally, the petiolar segments of *G. bezonnaisensis* (Fig. 215) and *P. agapa* (Fig. 184) are of similar length, though this is not a generic feature.

We base our morphological concepts of the taxon containing *P. agapa* mostly on the holotype of *P. agapa*, supplemented by similar specimens in Burmese amber (particularly GPPC: HY17A and AMNH: B-0107). Additional, better preserved specimens from French Bezonnais amber are required to definitively resolve the generic status of *G. bezonnaisensis* relative to *P. agapa*. Because the two taxa could be congeneric, we transfer *P. agapa* to *Galloromma* and classify *Galloromma* and its two currently described species, *G. bezonnaisensis* and *G. agapa* (Kozlov and Rasnitsyn) **n. comb.** in the family Gallorommatidae **n. fam.** We classify other extinct and extant mymarommatoids in Mymarommatidae (Table 1), as justified below.

*Classification of Mymarommatidae.*—No known autapomorphies support monophyly of *Archaeromma* and our study was insufficient to differentiate males from those of Tertiary and extant mymarommatid genera. We distinguish *Archaeromma* only by females having three or four compact claval segments (9: 0/1). The maxillae and labium may have been completely or almost completely separated in *Archaeromma* (Fig. 203), but this structure undoubtedly is symplesiomorphic. Furthermore, some species of *Mymaromella* have the maxillae and labium differentiated over much of their length (Fig. 44). Of the extant genera, monophyly of *Zealaromma* is well supported by the absence of metasomal spiracles (26: 1) and cerci (27: 1), presence of bumps on the posterior surface of the femora, particularly the mesofemur (24: 1), and likely by sclerotization (secondary) of the spiracular peritreme (20: 1). The 2-segmented female

clava (9: 2) of *Zealaromma* is enigmatic. The absence of both s4-type and s3-type sensilla from the basal claval segment (Fig. 71) might indicate that this segment evolved through autapomorphic secondary subdivision of a 1-segmented clava. Alternatively, the female claval structure could indicate *Zealaromma* constitutes a clade that is basal to *Palaeomymar* and other known Tertiary and extant species. Presence of external parameres in male *Zealaromma* (28: 0; Figs 154–156) and their absence from males of *Mymaromma* and *Mymaromella* (28: 1) indicates that *Zealaromma* is at least the sister taxon of these two extant genera. The absence of parameres recorded for *Palaeomymar* (28: 1) is based on only a single fossil and requires verification. The separate metanotum of *Z. valentinei* (16: 0; Figs 105, 106) may represent a third uniquely retained symplesiomorphy among extant mymarommatids. The two different structures of the meta-thoracic-propodeal complex that characterize *Mymaromma* (16: 1; Figs 82–84) and *Mymaromella* (16: 2; Figs 97–102), and the autapomorphic structure of *Z. insulare* (16: 3; Figs 109, 110), are hypothesized to have evolved through independent fusions of the metanotum with one or both of the metapleuron and propodeum. Among extant species, the posterior margin of the forewing of *Z. valentinei* also uniquely has several quite long setae basally (22: 0; Fig. 165). This setal pattern is similar to that of *Galloromma* (Fig. 188) and some *Archaeromma* (Fig. 194), suggesting a fourth uniquely retained symplesiomorphy among extant mymarommatids. We consider the structures discussed above as strong evidence that *Zealaromma* represents a monophyletic clade basal to *Palaeomymar*, *Mymaromma* and *Mymaromella*. The two known species of *Zealaromma* share a more internalized galea with *Mymaromma* (8: 1) and a completely fused meso- and metapleuron (15: 1) with most *Mymaromma*. They also have four supraclypeal setae (5: 0) and lack a metapleural pit (17: 1) similar

to most *Mymaromella*, but we consider these shared states either as symplesiomorphies or independently derived (see further below).

The best evidence for monophyly of *Mymaromma* is the presence of a  $\cap$ -like propodeal flange (19: 1; Figs 81, 87) that surrounds the insertion of the first petiolar segment into the propodeal foramen. Monophyly may also be supported by fusion of the metanotum laterally with the metapleuron (16: 1), which results in the spiracular peritreme forming an abrupt angle with the dorsal margin of the metapleuron (Figs 82–84). Although the holotype of *G. agapa* lacks this structure (Fig. 187), the spiracular peritreme is not clearly visible in *P. succini* or most other fossils. Species of *Mymaromma*, except for *M. sp. 9*, share two other apparently autapomorphic features — tridentate mandibles (3: 1; Figs 25–30) and a broad labium relative to the maxillae (7: 1; Figs 18–21). Individuals of *M. sp. 9* have bidentate mandibles (Fig. 31) and a comparatively narrow labium (Fig. 31, insert). *Mymaromma sp. 9* is also the only known species of *Mymaromma* having the meso- and metapleuron completely separated by a suture (15: 0; Fig. 82), but undoubtedly this is symplesiomorphic. A very fine suture also divides the meso- and metapleuron ventrally in *M. sp. 7* (Fig. 87), which indicates fusion of the meso- and metapleuron in *Mymaromma* evolved independently to similar fusion in *Zealaromma* (Figs 103, 108). Finally, *M. sp. 9* is the only observed species of *Mymaromma* having lateral setae on the first petiolar segment (state 25: 0; cf. Figs 92, 93, 104). However, because of the condition of specimens we were unable to survey this feature comprehensively and are not confident of the character-state distribution given for *Mymaromma* and *Mymaromella*. We did not observe petiolar setae in any fossil mymarommatid, but are uncertain whether this is because the setae are absent or too small to be visible. *Mymaromma sp. 9*

is indicated as the sister species of all other *Mymaromma* based on the features discussed above and is uniquely characterized by an extremely long, slit-like spiracular aperture (21: 1; Fig. 82: spa).

The monophyly of *Mymaromella* is not well established. Fusion of the metanotum posterolaterally to the propodeum (16:2) may support monophyly, but the exact structure of the metanotal-propodeal complex of *P. succini* and other fossils is unknown. The presence of paramedial setae on the occipital plate (4: 1; Figs 45, 46) and a metapleural pit about midway between the ventral margin of the pleuron and propodeal spiracle (18:1; Fig. 97: pl<sub>3</sub>p) could also support monophyly, but again these features could not be observed confidently in fossil mymarommatids and polarity is uncertain. Among extant mymarommatids, *Mymaromella* is most variable in the number and position of s4-type sensilla. Females of *Zealaromma* (Fig. 71) and *Mymaromma* (Figs 58, 59) have two s4-type sensilla (12: 0) near the dorsal margin of the outer surface (13: 0), whereas *Mymaromella* females have two or three such sensilla (12: 1; Figs 62, 63, 65, 67, 69) more or less medially (13: 1; Figs 63, 65, 67, 69) or sometimes in the dorsal third (Fig. 62). These character-state distributions suggest that the more ventral position of the sensilla is synapomorphic for *Mymaromella* and that presence of a third sensillum supports a monophyletic subgroup of *Mymaromella*. These hypotheses could be tested by a phylogenetic analysis of the species of *Mymaromella* and by determining the number and position of s4-type sensilla in fossil taxa. At least the apical three claval segments of female *Galloromma* have long, basally curved, robust sensilla (Figs 181, 182). Because of their length, these sensilla most closely resemble s2-type sensilla of extant mymarommatids (Figs 63, 70), but further study is necessary to determine if any of the sensilla originate from circular depressions. If so, they likely are homologous with s4-type sensilla.



The relationships of *Palaeomyrmar* with *Mymaromma* and *Mymaromella* are also not well substantiated. *Palaeomyrmar* is recognized as a separate genus because *P. succini* has a short, straight protibial calcar (23: 1; Fig. 210) similar to *Mymaromma* (Figs 142, 144a, 145a), but lacks the  $\cap$ -like propodeal flange (19: 0) that supports monophyly of *Mymaromma*. Individuals of *P. succini* also have all the setae along the posterior margin of the forewing short basally (22: 2; Figs 208, 209) similar to some species of *Mymaromella* (Figs 117, 166). A single conspicuously long posterobasal marginal seta (22: 1) is possessed by some species of *Archaeromma* (Figs 195, 202), other Tertiary fossils (Fig. 211), some *Mymaromella* (Figs 118, 119), and known *Mymaromma* (Figs 113, 114, 163) except *M. sp. 10*. Because of this character-state distribution, we consider the lack of a conspicuously long posterobasal marginal seta to be derived in *P. succini* and some *Mymaromella*. If this shared feature results from common ancestry then the reduced foretibial calcar shared by *P. succini* and *Mymaromma* must be independently derived. We consider it more likely that a long posterobasal marginal seta was lost independently from *P. succini* and within *Mymaromella* and that a reduced protibial calcar supports monophyly of *Palaeomyrmar* + *Mymaromma*. A phylogenetic analysis of the extant species of *Mymaromella* to establish the groundplan state of the marginal setae could test these hypotheses. Monophyly of *Palaeomyrmar* + *Mymaromma* may also be supported by fusion of the propleura into a carapace (14: 1; Fig. 18), though further study is necessary to verify character-state distribution in *Palaeomyrmar* as well as *Mymaromma* and *Mymaromella*. A 6-segmented funicle characterizes females and males of *Mymaromma goethei* (11: 1; Figs 174–176) and at least females of *P. succini* (Fig. 179). We consider that this similarity likely results from independent loss of a funicular segment in the two taxa. The phylogenetic position of *P. succini*

could be established more confidently by further study to provide missing data, particularly the exact structure of its metathoracic-propodeal complex.

Based on the above analysis, we currently consider the likely generic relationships of Mymaromatidae as *Archaeromma* + (*Zealaromma* + (*Mymaromella* + (*Palaeomyrmar* + *Mymaromma*))) (Fig. 1).

### Mymarommatoidea

*Description*.—Antennae geniculate, inserted subcontiguously at or above middle of face; flagellum without multiporous plate sensilla. Female antenna with 9–13 segments including a variably structured clava composed of 1–4 segments; clava with short, peg-like sensilla along ventral midline (Figs 72, 181b), long, robust, basally curved sensilla on dorsal and/or outer surface (Figs 58, 63, 181, 182), and at least extant members with 2 or 3 short, basally curved lanceolate sensilla originating from depressions on outer surface (Figs 59, 65, 69, 70). Male antenna 12- or 13-segmented, with the apical 2–4 segments often somewhat coalesced as an indistinct clava, but the flagellum more or less filiform; fl<sub>9</sub> and fl<sub>10</sub> or fl<sub>8</sub>–fl<sub>10</sub> each with short, basally curved lanceolate sensillum originating from depression distally. Ocelli present or absent. Pronotum with postero-dorsal margin not extending to base of forewing and its posterior margin not rigidly interlocked with anterior margin of mesopleuron. Propleura forming exposed lateral and ventral portions of propectus, with ventral margins abutting medially or fused to varying extent. Prosternum vertical, largely concealed between posterior margin of propleura and base of procoxae. Functional mesothoracic spiracle absent. Prepectus not externally visible. Tegula absent. Mesoscutum with distinctive scabrous sculpture, without notauli or median mesoscutal sulcus; scutellum composed of convex anterior scutellum and slightly concave, transverse, longitudinally

strigose posterior scutellum; anterior scutellum without differentiated dorsal axillar regions. Metanotum an independent sclerite or fused with one or both of metapleuron and propodeum. Mesopleuron and metapleuron separated by oblique suture or partly to entirely fused. Forewing humeral plate bare. Forewing pedunculate, stalk-like basally and disc broadly spatulate to lanceolate; disc membrane with mesh-like pattern formed by raised lineations on both surfaces; marginal setae, when long, arising distinctly from within periphery of disc apically; venation strongly reduced within basal quarter of wing, consisting of submarginal, marginal and very short stigmal vein delimited apically by a campaniform sensilla and projecting seta. Hind wing stalk-like, terminated by

single hamulus and opposing projection that together form pincer-like structure. Legs with tarsi 5-segmented; protibial calcar straight and simple or curved and bifurcate; meso- and metatibiae of at least extant members without tibial spurs; mesocoxa with basicoxite reduced to small dorsal lobe projecting into mesocoxal foramen, and mesotrochantal lobe not externally visible. Metasoma 8-segmented with first two segments tubular; post-petiolar segments with terga broadly overlapping sterna without differentiated laterotergites. Female with hypopygium extending to apex of metasoma and therefore often concealing ovipositor, but apex capable of wide separation from syntergum; ovipositor non-telescoping, extended ventrally from gaster by rotation.

KEY TO FAMILIES AND GENERA OF MYMAROMMATOIDEA

- 1. Cretaceous; female flagellum with 7 funicular segments and 3- or 4-segmented clava (Figs 180, 182, 189, 190, 196, 199, 200, 204) ..... 2
- Tertiary or extant; female flagellum with 6 or 7 funicular segments and 1-segmented clava (Figs 173–175, 178, 179) or 7 funicular segments and 2-segmented clava (Figs 71, 172) ..... (Mymarommatidae, part) 3
- 2(1) Head capsule uniformly sclerotized and with vertex smoothly rounded into concave occiput (Fig. 186); mandibles not exodont (Figs 189, 190, 191, 193), thin, curved mesally and broadly overlapping when closed; clava of female consisting of 4 distinctly separated segments (Figs 180, 182, 189, 190) ..... *Galloromma* Schlüter (Gallorommatidae **n. fam.**)
- Head capsule with hyperoccipital band of pleated membrane separating frontal plate from flat occipital plate (cf. Figs 13, 14) or frontal plate abruptly angled or hood-like relative to occipital plate if this rotated anteriorly (Fig. 198, cf. Fig. 15); mandibles exodont (Figs 197, 198), comparatively broad with concave outer surface and apices not meeting medially when closed (cf. Figs 31, 47–49); clava of female consisting of 3 or 4 segments, but these separated by linear sutures and forming compact tube (Figs 192, 196, 199, 200, 204) ..... *Archaeoromma* Yoshimoto (Mymarommatidae)
- 3(1) Protibial calcar straight, simple (Figs 142, 144a, 145a); *extant taxa* with posterior margin of propodeum extending as  $\cap$ -like flange (Figs 86, 87) and concealing propodeal foramen in dorsal (Figs 78, 79) and lateral (Figs 80, 83) view ..... 4
- Protibial calcar apically curved and bifurcate (Figs 137–139a, 140); *extant taxa* with posterior margin of propodeum extending as variably distinct flange only laterally on either side of short, protruding, tubular foramen (Figs 90–97, 104, 107) ..... 5
- 4(3) Posterior margin of forewing with several short setae separating conspicuously long basal seta from longer apical setae (Figs 113–115); propodeum with  $\cap$ -like flange (Figs 86, 87) concealing foramen in dorsal and lateral view; mesopleuron and metapleuron usually partially (Fig. 87) or completely fused (Fig. 80), only very rarely completely separated by oblique suture (Fig. 82). Extant ..... *Mymaromma* Girault

- Posterior margin of forewing with all setae short basally (Figs 207–209); propodeum without distinct  $\cap$ -like flange, the foramen projecting as short tube anterior to petiolar insertion (cf. Fig. 94); mesopleuron and metapleuron separated by oblique suture (cf. Figs 97, 99). Extinct (Baltic amber) . . . . . *Palaeomymar* Meunier
- 5(3) Mesopleuron and metapleuron fused together (Figs 103, 108); Mt<sub>7</sub> without spiracles (Fig. 154); mesofemur with row of bumps on posterior surface (Fig. 146b); female clava 2-segmented (Fig. 172) . . . . . *Zealaromma* n. gen.
- Mesopleuron separated from metapleuron by diagonal suture (Figs 95– 97, 99, 101); Mt<sub>7</sub> with spiracles (Figs 149–152, 158); mesofemur without bumps on posterior surface; female clava 1-segmented (Fig. 178) . . . . . *Mymaromella* Girault

**Gallorommatidae<sup>†</sup> n. fam.**

*Type genus.*—*Galloromma* Schlüter, present designation.

*Diagnosis.*—Distinguished from *Mymarommatidae* by the following features. Head capsule uniformly sclerotized and sculptured, with convex vertex smoothly rounded into medially concave occiput (Figs 186, 213); occipital foramen originating from middle of occiput. Mandible not exodont (Figs 189, 190, 193); when closed, apices of mandibles broadly overlapping (Fig. 189) and dorsal margin distinctly separated from oral margin of head capsule. Female antenna with 13 distinct segments, including 7 funicular segments and 4 larger apical segments that are distinctly separated to form a loose clava (Figs 180, 182, 189, 190, 214).

***Galloromma*<sup>†</sup> Schlüter**

*Galloromma* Schlüter, 1978: 74–76. Type species: *Galloromma bezonnaisensis* Schlüter; original designation.

*Description.*—In addition to the diagnostic features given above for the family, other features that are not visible in all inclusions but that likely characterize *Galloromma* are as follows. Head with ocelli (Fig. 186); eye large, with numerous ommatidia (Fig. 186); toruli near level of center of head and eyes (Fig. 183); mandible with subbasal tooth (Figs 191, 193). Protibial calcar conspicuously long,

curved, and apically bifurcate (insert, Figs 183, 191). Propleura divided medially. Mesopleuron and metapleuron separated by complete suture; metapleuron with large pit about midway between propodeal spiracle and ventral margin of pleuron (Fig. 187). Propodeum with spiracle near posterior margin of scutellum (Fig. 187) and without distinct  $\cap$ -like flange surrounding foramen (Figs 184, 187). Forewing disc spatulate (Fig. 183) with two longitudinal folds, the membrane with comparatively numerous, scattered, short setae; posterior margin with setae all of similar length basally (Figs 191, 216) or with at least three moderately long setae proximal to shorter setae (Figs 188, 194).

*Included species.* —*Galloromma agapa* (Kozlov and Rasnitsyn), n. comb. *Palaeomymar agapa* Kozlov and Rasnitsyn, 1979: 414–415. Holotype ♀, PIN (examined).  
*Galloromma bezonnaisensis* Schlüter, 1978: 74–76. Holotype ♀, ZMB (examined).

***Mymarommatidae***

*Type genus.*—*Mymaromma* Girault, 1920: 38.

*Diagnosis.*—Distinguished from *Gallorommatidae* by the following features. Head capsule with  $\cap$ -shaped hyperoccipital band of pleated membrane differentiating flat occipital plate from convex frontal plate (Figs 13, 14, 42); occipital foramen

originating at ventral margin of occipital plate. Mandibles exodont; when closed, their apices not meeting and dorsal margins abutting oral margin of head capsule (Figs 28–31, 47–49). Female antenna with 9–11 distinct segments, including 6 or 7 funicular segments and 1 or 2 claval segments (Figs 172–175, 178, 179) or if with 3 or 4 claval segments then these forming a compact tube with only basal two segments separated by distinct suture (Figs 192, 196, 200, 204).

*Remarks.*—Huber (2005) discussed the derivation and gender of the generic names.

### *Archaeomomma*<sup>†</sup> Yoshimoto

*Archaeomomma* Yoshimoto, 1975: 503. Type species: *Ooctonus minutissimus* Brues; designated by Yoshimoto (1975: 503).

*Protooctonus* Yoshimoto, 1975: 511. Type species: *Protooctonus masneri* Yoshimoto; original designation. **n. syn.**

*Diagnosis.*—Females are distinguished from other Mymarommatidae by their compact clava consisting of at least three, sometimes possibly four, coalesced segments.

*Included species.*—*Archaeomomma japonicum* (Fursov, Shirota, Nomiya and Yamagishi), **n. comb.** *Palaeomymar japonicum* Fursov, Shirota, Nomiya and Yamagishi, 2002: 52–54. Holotype ♂, Y. Shirota collection, Laboratory of Evolutionary Ecology, Faculty of Agriculture and Life Sciences, Hirosaki University, Japan.

*Archaeomomma mandibulatum* (Kozlov and Rasnitsyn), **n. comb.** *Palaeomymar mandibulatus* Kozlov and Rasnitsyn, 1979: 413–414. Holotype ♀, PIN (examined).

*Archaeomomma masneri* (Yoshimoto), **n. comb.** *Protooctonus masneri* Yoshimoto, 1975: 511–512. Holotype ♀, CNC (examined).

*Archaeomomma minutissimum* (Brues). *Ooctonus minutissimus* Brues, 1937: 44; combination by Yoshimoto (1975: 503). Holotype ♀, ROMT (examined).

*Archaeomomma nearcticum* Yoshimoto. *Archaeomomma nearctica* Yoshimoto, 1975: 506. Holotype ♀, CNC (examined).

*Archaeomomma senonicum* (Kozlov and Rasnitsyn), **n. comb.** *Palaeomymar senonicus* Kozlov and Rasnitsyn, 1979: 412–413. Holotype ♀, PIN (examined).

*Remarks.*—Our generic placement of *A. japonicum* is tentative because this species is based on a unique male and we distinguish *Archaeomomma* from other genera only by the claval structure of females. We classify it in *Archaeomomma* because of its age (about 85 mya) and because the illustrations provided with the original description are very similar to specimens from New Jersey amber that we assign to *Archaeomomma*.

When Yoshimoto (1975) established *Protooctonus* he stated that the forewing and female antenna “shows great similarity” to that of mymarommatids. He classified the genus in Mymarinae (Mymaridae) because he considered it had a subpetiolate gaster. The female holotype is crushed and the detached head is behind the mesosoma (Fig. 206). The dorsal surface of the mesosoma is clearly visible and structure and sculpture of both the mesoscutum (Fig. 206: msc) and scutellum (Fig. 206: asc + psc) is typical for mymarommatids. There is also a rod-like structure projecting obliquely from the anterolateral margin of the scutellum that almost certainly is an axillar phragma (Fig. 206: axp) and the toruli are subcontiguous and inserted high on the head (Fig. 206). In dorsal view, the posterior surface of the head (Fig. 196: ocp?) appears detached from the vertex and in lateral view the region has concentric lines dorsally (Fig. 206) similar to a hyperoccipital band of pleated membrane. What might be a 2-segmented petiole (Fig. 206: pt<sub>1</sub>, pt<sub>2</sub>) lies below the detached head anterior to a coxa. For these reasons, we transfer *Protooctonus* from Mymaridae to Mymarommatidae. We also synonymise *Protooctonus* under *Archaeomomma* because of the similar antennal structure of the type species (cf. Figs 192, 196). The two males designated as paratypes of *P. masneri* by Yoshimoto (1975) are

not conspecific with the holotype female. The males represent an unidentified species of Mymaridae based on the presence of long, raised, multiporous plate sensilla on the flagellum (diagnostic of Chalcidoidea) and widely separated antennal toruli (diagnostic of Mymaridae).

***Palaeomymar*<sup>†</sup> Meunier**

*Palaeomymar* Meunier, 1901: 289. Type species: *Palaeomymar succini* Meunier; original designation and monotypy.

**Diagnosis.**—Distinguished from other Mymarommatidae by the following combination of features. Head with ocelli. Mandible bidentate. Labiomaxillary plate with labium about as wide as maxilla. Female antenna 9-segmented with 6-segmented funicle and 1-segmented clava (Fig. 179); male antenna 12-segmented with 6-segmented funicle and 4-segmented clava (cf. Fig. 177). Propleura fused into carapace. Protibial calcar short and straight (Fig. 210). Forewing disc with hair-like setae; posterior margin with short marginal setae over basal half (Figs 207–209). Propodeum posteriorly without complete,  $\cap$ -like flange, the foramen protruding as short tube (cf. Fig. 94). Male genitalia lacking externally projecting parameres.

**Included species.**—*Palaeomymar succini* Meunier, 1901: 289–290.

**Remarks.**—As discussed above, Duisburg (1868) originally had 13 males and 3 females of which Meunier (1901) examined five males when he established *P. succini*. He obtained the type material from the “Musée Provincial de Königsburg” (Albertus Universität in Königsberg). According to Grimaldi and Engel (2005) most of the material stored in the museum was lost or destroyed during World War II, although a surviving portion is preserved in GZG. Search of the GZG Baltic amber collection by its curator, M. Reich, failed to locate any material identified as *P. succini*, and our survey of their unidentified Baltic amber Hymenoptera failed to

recover any mymarommatids. The slide-mounted male labelled “33059 Kl.” from the GZG “Klebs” collection (see discussion of Tertiary fossils) could not have been one of the five males examined by Meunier (1901). He stated that “embrowning” of the forewings prevented observation of the structure of the “nervus ulnerus” and both wings of the Klebs collection male are perfectly clear within the amber piece.

Because we distinguish three genera for the extant species, all of which are classified in *Palaeomymar*, it is necessary to designate a neotype for *P. succini* to fix use of the generic name. Based on correlated structure of the protibial calcar, forewing marginal setal pattern, and 9-segmented antenna in females, we identify in the ZMUC collection what we believe are associated sexes of the species that was discussed and illustrated by Duisburg (1868) and Meunier (1901). We designate a male as neotype because the original type series of Meunier (1901) consisted only of males and the neotype male is the only specimen that under a dissecting microscope clearly shows a short, straight (needle-like) protibial spine (Fig. 210: ca?). This spine almost certainly is the calcar, but absence of a long, curved calcar is indicated even if it is only a pseudospur (cf. Fig. 143: ps). The marginal setae of the forewings are also visible in the male selected and clearly show that the basal setae are all very short (Figs 207, 208). It is easier to differentiate *P. succini* from other species in Baltic amber based on females than males because of additional antennal features. We therefore also provide descriptive features for the ZMUC female labelled as 16-1/1961, which is the best preserved of all the specimens. It is almost the same size as the neotype male and also lacks a long protibial calcar.

**Neotype designation:** *Neotype data:* Fossil male, deposited in ZMUC with the following label data: two white labels with “Vesterhav, S. Nielsen, Skjolddelev, Min. Mus. [Mineralogisk Museum] 1890-108”

and "Mymarommidae Mymaromma: O.B. 1964", plus our red neotype label with "Neotype *Palaeomymar succini* Meunier, 1901 designated by Gibson, Read and Huber".

The maximum size of the amber block containing the neotype is  $5.5 \times 3.75 \times 3.25$  mm, though it narrows slightly in all dimensions in the direction toward the dorsal surface of the specimen. The sides of the block are smooth except one side has a missing section, which partly obscures observation of the specimen in ventrolateral view. The specimen is obliquely angled with the head directed more or less dorsally (Fig. 207) when the block is set on its side with the missing section.

*Neotype description*.—Male. Body length about 0.35 mm excluding antennae (length probably underestimated slightly because of foreshortening). Forewing 0.36 mm long  $\times$  0.12 mm wide; marginal fringe with longest setae as long as maximum wing width, the exact number of marginal setae uncertain but with about 15 shorter setae along posterior margin basally (these setae increasing in length distally) and about 35–40 much longer setae over apical half; disc membrane longitudinally convoluted. Head with ocelli.

*Female description*.—Antenna (Fig. 179) with combined length of pedicel and flagellum subequal to body excluding second petiolar segment and gaster; scape 4x as long as wide and 1.6x as long as pedicel; relative length of pedicel: funicle: clava = 1: 4: 3; funicle with basal four segments tubular, apical two segments increasingly more distinctly widened ventrally, and apical segment with dorsal attachment to base of clava; clava 3.75x as long as wide, the dorsal margin apparently without strong bent sensilla. Face very finely sculptured, shiny; malar space distinct. Eye moderately large, with numerous ommatidia. Mandibles comparatively slender, closed with apices apparently widely separated medially. Mesosoma with complete but fine metapleural suture; propo-

deum posteriorly without complete  $\cap$ -like flange, the foramen protruding as short tube that is longer ventrally than dorsally; in lateral view, first petiolar segment with basal constriction clearly visible and inserting into tubular propodeal foramen, the segment subequal in length to metacoxa and twice as long as second petiolar segment. Forewing elongate-spatulate, 1.4x as long (measured from apex of venation) as maximum width, with about 15 shorter setae basally along anterior margin, about 45 much longer setae distally along anterior, apical and posterior margins, and an uncertain number of shorter setae along posterobasal margin.

### *Mymaromma* Girault, revised status

*Mymaromma* Girault, 1920: 38. Type species: *Mymaromma goethei* Girault; original designation. Synonymy under *Palaeomymar* Meunier by Doutt (1973: 225).

*Petiolaria* Blood and Kryger, 1922: 229. Type species: *Petiolaria anomala* Blood and Kryger; by monotypy. Synonymy under *Mymaromma* by Girault (1930: 4).

*Description*.—Head with or without ocelli; interorbital region of face with 10 setae, including 2 setae paramedially above oral margin (Figs 18, 20); occipital plate bare except for ventrolateral seta at each corner (Figs 14, 23, 42). Mandible usually tridentate with variably large and distinct subapical angle or tooth projecting above oral margin (Figs 26–30), though rarely bidentate (Fig. 31). Labiomaxillary plate with labium about twice as wide as maxilla (Figs 19–22, 28) except very rarely (Fig. 31, insert); maxilla with palpal spine apically on stipes and with galea internalized and apically pustulate (Figs 19–22). Female flagellum with 6 or 7 funicular segments and 1-segmented clava; clava with 2 s4-type sensilla on outer surface near dorsal margin (Figs 58, 59). Male flagellum 12- or 13-segmented with single s4-type sensillum apically on fl<sub>9</sub> and fl<sub>10</sub> (Figs 60, 61). Propleura fused into carapace (Fig. 18). Mesopleuron and metapleuron usually

fused (Figs 80, 81, 83), rarely partly (Fig. 87: mms) or completely separated by suture (Fig. 82), but with curved furrow extending from posteroventral margin of mesothorax to distinct metapleural pit near propodeal spiracle (Figs 81, 87). Metathoracic-propodeal complex with metapleuron, at least dorsally, distinctly smoother than more coarsely sculptured propodeum (Figs 80–83); spiracular aperture oval to slit-like and connected to anterior margin of propodeum by slit-like peritreme, in lateral view the peritreme and dorsal margin of metapleuron forming acute angle directed between scutellum and propodeum (Figs 82–84); metanotum separated from propodeum by peritreme but fused with metapleuron (Fig. 84); pre-spiracular setae within angle formed by dorsal margin of metanotum and peritreme (Figs 84, 85) and postalar sensillum at extreme dorsal margin of metapleuron (Figs 84, 85). Propodeum posteriorly reflexed into  $\cap$ -like flange over petiolar insertion, the posteroventral margin of flange and projection of metapleuron forming pincer-like structure (Figs 81, 83, 86, 87). Forewing often appearing more or less lanceolate, the disc longitudinally convoluted with hair-like setae aligned along folds on dorsal and ventral surfaces (Figs 113–115), and sometimes densely hairy if setae very long (Fig. 116); posterior margin usually with basal seta conspicuously longer than adjacent short setae (Figs 113–115). Femora without bumps on posterior surface. Protibial calcar short, straight and simple (Figs 142, 144a, 145a). Metasoma with  $Mt_1$  longer than  $Mt_2$  but their relative length variable;  $Mt_1$  dorsally variable in sculpture, almost smooth (Fig. 83) to strongly reticulate (Fig. 88), and only very rarely with lateral seta;  $Mt_2$  finely sculptured, usually almost smooth (Fig. 83);  $Mt_7$  with spiracle and seta mesal to spiracle (Fig. 152); syntergum with cerci, the cercus differentiated as subcircular structure (*cf.* Fig. 150) or variably fused with tergite as part of its surface (Fig. 152),

and with 1–4 setae. Male genitalia without externally evident parameres.

*Included species.*—*Mymaromma anomalum* (Blood and Kryger), **rev. comb.** *Petiolaria anomala* Blood and Kryger, 1922: 229–230. Holotype ♂, BMNH (not examined).

*Mymaromma buyckxi* Mathot, 1966: 236–237, **rev. comb.** Holotype ♀, ISNB (examined).

*Mymaromma goethei* Girault, 1920: 38–39, **rev. comb.** Holotype ♀, QMBA (examined).

*Mymaromma mirissimum* (Girault), **n. comb.** *Mymaromella mirissima* Girault, 1935: 3. Holotype ♀, QMBA (examined).

*Mymaromma ypt* (Triapitsyn and Berezovski), **n. comb.** *Palaeomymar ypt* Triapitsyn and Berezovski, 2006: 5–7. Holotype ♀, Zoological Museum of Moscow State University, Moscow, Russia (not examined). Paratype ♀ and ♂, CNC (examined).

*Distribution.*—We have seen individuals and/or species have been reported in the literature from the following areas: **Afro-tropical** — Congo (Mathot 1966), Gabon, Madagascar, Nigeria. **Australasian** — Australia (Girault 1920), Chatham Island, Christmas Island, Hawaii (Beardsley et al. 2000), Indonesia (Ceram), New Caledonia, New Zealand, Norfolk Island, Papua New Guinea. **Nearctic** — Canada, Mexico. **Neotropical** — Bermuda, Brazil, Colombia. **Oriental** — China (Lin 1994) [Fujian, Yunan], Indonesia [Kalimantan, Sulawesi, Sumatra], Malaysia [Sabah], Nepal, Philippines (Gallego 1986), Taiwan, Thailand. **Palearctic** — Belgium (Debauche 1948), Bulgaria (Donev 1982), Czech Republic (Kalina 1989), Denmark (Blood and Kryger 1936), England (Blood and Kryger 1922), France, Germany (Vidal 2001), Hungary, Italy (Viggiani 1966), Japan, Norway (Hansen 1997), Poland (Soyka 1937), Romania (Andriescu and Suciu 1963), Russia (Triapitsyn and Berezovski 2000), South Korea (Triapitsyn and Berezovski 2006), Spain (Askew et al. 2001), Sweden, Switzerland (Ferrière 1948).

*Remarks.*—All described species are extant, but species likely existed in the Tertiary.



### *Mymaromella* Girault, revised status

*Mymaromella* Girault, 1931: 4. Type species: *Mymaromella mira* Girault; by monotypy. Synonymy under *Mymaromma* Girault by Annecke and Doutt (1961: 14) and under *Palaeomyrmar* Meunier by Doutt (1973: 225).

**Description.**—Head with or without ocelli; interorbital region of face with 6–10 setae, including 2 (Fig. 36) or 4 (cf. Fig. 56) setae above oral margin; occipital plate with 2 paramedial setae (Figs 45, 46: ms) in addition to ventrolateral seta at each corner. Mandible bidentate with both teeth acutely angled (Figs 34, 48, 49), the dorsal tooth much longer than ventral subapical tooth. Labiomaxillary plate with labium narrow, only about as wide as maxilla (Figs 41, 41, 44, 47–49); maxilla with palpal spine subapical and with galea a longer, fleshy lobe exterior to spine (Fig. 41). Female flagellum with 7 funicular segments and 1-segmented clava; clava with 2 or 3 s4-type sensilla on outer surface near midline (Figs 62, 63, 65, 67, 69). Male flagellum 13-segmented with single s4-type sensillum apically on fl<sub>9</sub> and fl<sub>10</sub> or fl<sub>8</sub>–fl<sub>10</sub> (corresponding to number of sensilla on female clava) (Figs 66, 68). Propleura abutting medially or at least distinguished by median line of differentiated sculpture (Figs 43, 44). Mesopleuron and metapleuron separated by suture (Figs 95–97, 99, 101), without a distinct metapleural pit though sometimes with a very tiny hole about midway between ventral margin of pleuron and propodeal spiracle (Figs 97, 101), and without curved furrow extending dorsally from posteroventral margin of mesothorax. Metathoracic-propodeal complex with sculpture of propodeum and metapleuron quite similar even if pleural sculpture somewhat finer (Figs 95–97, 99, 101); spiracular aperture circular to oval and connected to anterior margin of propodeum by slit-like peritreme, in lateral view the peritreme and dorsal margin of metapleuron forming evenly convex arc (Figs 95–102); metanotum fused with pro-

podeum, but separated from metapleuron by peritreme such that metanotal-propodeal complex form variably long angle directed anteriorly between scutellum and dorsal margin of metanotum (Figs 98, 100, 102); prespiracular setae within dorsolateral angle of metanotal-propodeal complex and postalar sensillum either at extreme anterior angle of complex (Figs 98, 100) or sometimes appearing anterior to it (Fig. 102). Propodeum posteromedially constricted into short tube anterior to reflexed foraminal margin (Figs 90–97, 99, 101), and with posterolateral margin more or less distinctly reflexed as flange on either side of constriction (Figs 92, 94: pf) to form pincer-like structure with projection of metapleuron (Figs 92, 94, 96, 97, 101). Forewing variable in shape (Figs 117–121) though often spatulate (Fig. 119) or broadly rounded apically (Figs 118, 166), the disc with or without distinct longitudinal convolutions but with short, spine-like setae; length of marginal setae highly variable and posterior margin with (Figs 118, 1119) or without (Figs 117, 120, 166, 121) a conspicuously long basal seta. Femora without bumps on posterior surface. Protibial calcar long, apically curved and bifurcate (Figs 137–139a). Metasoma with Mt<sub>1</sub> longer than Mt<sub>2</sub> but their relative length variable; Mt<sub>1</sub> dorsally more or less transversely strigose-coriaceous and with lateral seta within basal half (Figs 90, 92, 94); Mt<sub>2</sub> variable in sculpture dorsally, usually transversely strigose; Mt<sub>7</sub> with spiracle and seta mesal to spiracle (Figs 149–151); syntergum with cerci, the cercus differentiated as subcircular structure (Figs 149–151) or variably fused with tergite as part of its surface (cf. Fig. 152), and with 2–4 setae. Male genitalia without externally evident parameres.

**Included species.**—*Mymaromella chaoi* (Lin), **n. comb.** *Palaeomyrmar chaoi* Lin, 1994: 123–124. Holotype ♀, FAUF (not examined).

*Mymaromella cyclopterus* (Fidalgo and De Santis), **n. comb.** *Palaeomyrmar cyclopterus*

Fidalgo and De Santis, 1982: 3–4. Holotype ♀, MLPA (examined).

*Mymaromella duerrenfeldti*\* (Schlüter and Kohring), **n. comb.** *Palaeomymar duerrenfeldti* Schlüter and Kohring, 1990: 117–118. Holotype ♂, ZMB (examined).

*Mymaromella mira* Girault, 1931: 4. **rev. comb.** Holotype ♀ photograph, QMBA, USNM (examined).

**Distribution.**—We have seen individuals and/or species have been reported in the literature from the following areas: **Afro-tropical** — Ivory Coast. **Australasian** — Australia (Girault 1931). **Nearctic** — Canada (Clouâtre et al. 1989), United States. **Neotropical** — Argentina (Fidalgo and De Santis 1982), Brazil, Trinidad, Venezuela (reported as *Palaeomymar* by García 2000). **Oriental** — China (Fujian, Guangxi). **Pa-laeartic** — South Korea (Triapitsyn and Berezovskiy 2006), Sweden.

**Remarks.**—We newly classify *M. duerrenfeldti* in *Mymaromella* because of the relatively recent age (about 5 mya) of this Tertiary species and because it has bidentate mandibles, a long and curved protibial calcar, and broadly rounded forewings with short discal setae.

Lin (1994, fig. 4) illustrated the bidentate mandibles of *M. chaoi* as having a short dorsal tooth and a long ventral tooth. Study of topotypic material shows this to be erroneous and the short tooth is ventral as in other *Mymaromella*.

*Mymaromella mira* was described from a photograph of a female “collected at Canterbury, Victoria in April” (Dahms 1984), which is in the QMBA. According to Girault’s unpublished manuscript, the photograph is the “type” and a “paratype” photograph dated “January 4, 1931 (4-1-31)” that was sent to the USNM (Dahms 1984). The USNM photograph (Fig. 168) is identical to the QMBA photograph and has the data “[?] Girault letter to Gahan Nov. 1934”. Because the two photographs are identical this suggests that *M. mira* was based on a unique specimen. The discrepancy between the collection date of the

“type” and the date given for the “paratype” may simply reflect the date the photographs were printed or perhaps is a misinterpretation of the month *vs.* the day, i.e., “4-1-31” either representing April 1 or 4 January, 1931. Close examination of the photographs show that there is a comparatively long posterobasal seta on the forewings (*cf.* Fig. 118).

### *Zealaromma* n. gen.

**Type species.**—*Mymaromma insulare* Valentine, 1971: 331–333; present designation.

**Etymology.**—A combination of New Zealand, the only country from which species of the genus are known, and *Mymaromma*, the genus in which the type species was first described.

**Description.**—Head with or without ocelli; interorbital region of face with 8 setae, including 4 setae above oral margin (Fig. 56); occipital plate bare except for ventrolateral seta at each corner (Fig. 50). Mandible bidentate with both teeth acutely angled and dorsal tooth much longer than ventral subapical tooth (Figs 52, 54). Labiomaxillary plate with labium narrow, only about as wide as maxilla (Figs 50, 52); maxilla with palpal spine apical on stipes and with galea internalized and apically pustulate (Figs 55–57). Female flagellum with 7 funicular segments and 2-segmented clava (Figs 71, 172); terminal claval segment with 2 s4-type sensilla on outer surface near dorsal margin (Fig. 71). Male flagellum 12-segmented with single s4-type sensillum near apex of fl<sub>9</sub> and fl<sub>10</sub> (Fig. 73). Propleura abutting medially. Mesopleuron and metapleuron fused except for short suture below base of forewing, without evident metapleural pit, but with shallow groove extending dorsally from posteroventral margin of mesothorax to propodeal spiracle (Figs 103, 108). Metathoracic-propodeal complex with distinct smooth region between much more coarsely sculptured propodeum and metapleuron ventrally (Figs 104, 107, 108);

spiracular peritreme circular and without slit-like peritreme between aperture and anterior margin of propodeum; metanotum either independent from both propodeum and metapleuron (Figs 105, 106) or fused with propodeum and metapleuron (Figs 109, 110), but with postalar sensillum (Figs 105, 110: pas) separated from apparent "metanotum" anterior to prespiracular setae (Figs 105, 110: pss). Propodeum posteromedially constricted into short tube anterior to reflexed foraminal margin (Figs 103, 104, 107, 108), and with posterolateral margin reflexed as distinct vertical flange beside tubular constriction (Figs 104, 107). Forewing variably distinctly spatulate (Fig. 165) to lanceolate (Figs 122, 164), but disc longitudinally convoluted and with hair-like setae aligned along folds on dorsal and ventral surfaces; marginal setae comparatively short and stiff (spine-like) (Figs 122, 164) or very long and hair-like (Fig. 165), the posterobasal seta sometimes long but if so then not distinctly differentiated in length from adjacent setae (Fig. 165). Femora, particularly mesofemur, with bumps on posterior surface (Fig. 146). Protibial calcar long, apically curved and deeply bifurcate with very long inner tine (Fig. 140). Metasoma with Mt<sub>1</sub> nearly twice as long as Mt<sub>2</sub>; Mt<sub>1</sub> with subbasal lateral seta (Fig. 104) and Mt<sub>1</sub> and Mt<sub>2</sub> dorsally very finely sculptured (Figs 104, 107); Mt<sub>7</sub> without spiracle

(Figs 153–155) and usually bare (Figs 153, 155); syntergum without cerci (Figs 153, 155). Male genitalia with elongate-digitiform paramere bearing long terminal seta projecting externally from between syntergum and hypopygium (Figs 154–156).

*Included species.*—*Zealaromma insulare* (Valentine, 1971), **n. comb.**

*Zealaromma valentinei* Gibson, Read and Huber, **n. sp.**

*Remarks.*—Valentine (1971) stated that he recognized five species from mainland New Zealand in addition to *Z. insulare*, which differed in the form and fusion of the mesothoracic segments, simple or divided clava, size and shape of the forewings (one being apterous), and presence or absence of ocelli. Noyes and Valentine (1989) also stated that there were five undescribed species in New Zealand, including a brachypterous and apparently an apterous species. We did not locate any brachypterous or apterous specimens and from the material we examined from New Zealand recognize only three species: *Z. insulare*, *Z. valentinei* and an undescribed species of *Mymaromma*. This species, *M. sp.* 10, is represented by a single female from the South Island (NZAC) and several other specimens (Appendix II) that differ from all other mymarommatids in their extremely long and dense forewing discal setae (Fig. 116).

KEY TO SPECIES OF ZEALAROMMA

- 1. Forewing with about 10 stiff, relatively short (needle-like) and widely spaced distal marginal setae originating from wing margin (Figs 122, 164); head without ocelli; metanotum fused with both metapleuron and propodeum (Figs 108–110) ..... *Zealaromma insulare* (Valentine)
- Forewing with numerous fine, very long (hair-like) and closely spaced distal marginal setae originating distinctly from within wing periphery (Fig. 165); head with ocelli (Fig. 53); metanotum separated from metapleuron and propodeum by sutures (Figs 105, 106) ..... *Zealaromma valentinei* **n. sp.**

*Zealaromma valentinei* n. sp.

*Type material*.—**Holotype**. Female. "NEW ZEALAND BR [South Island: Buller] Lake Rotoiti 610m; 26 Dec 1979 - 4 Jan 1980 A.K. Walker" / "Holotype *Zealaromma valentinei* Gibson, Read and Huber" (NZAC). **Paratypes** (15♀, 5♂). NEW ZEALAND, North Island: **ND** [Northland] Waipoua Kauri Forest, 11-12.XII.1983, L. Masner, s.s. (1♀ CNC). **TK** [Taranaki]: Mt. Egmont N.P., 16.XII.1983, L. Masner, s.s. (1♀ CNC). NEW ZEALAND, South Island: **BR** 1♀, same data as holotype (NZAC). Lower Buller R., Norris Ck., 14.X.1970, J.I. Townsend, litter 70/158 (2♀ on one card NZAC). Punakiki, 28.XII.1983, L. Masner, s.s. (1♀, 1♂ CNC). Tuttys Plateau, Mawhera, 20.IX.1972, J.S. Dugdale, moss 72/178 (1♀ NZAC). **MC** [Mid Canterbury], Banks Peninsula, Prices Valley, II.1981, R.P. Macfarlane, malaise trap, edge of native bush (1♀ NZAC). Banks Peninsula, Prices V, 19-27.X.1988, J.W. Early (5♀, 2♂ CNC; 1♀ gold coated for SEM). **NN** [Nelson], Wooded peak Dun Track Sdle, 14.IX.1971, G.W. Ramsay, litter 71/110 (1♀ NZAC). **SL** [Southland], Longwood Forest, Purakino picnic area, 24-28.I.1999, L. LeSage, Nothofagus forest, YPT 99-57 (1♀, 2♂ CNC).

*Etymology*.—Named in honour of Dr. Errol Valentine, who first published on New Zealand mymarommatoidea.

*Description*.—Length, 0.55 mm (air-dried holotype). Body yellow except small triangular region below base of forewing and ocellar triangle dark brown, gaster sometimes brownish dorsally; hind leg with apices of basal three tarsal segments very narrowly brown; forewing disc with middle third to basal half of mesh-like lineations and the marginal setae behind this region brown (Fig. 165).

Head with ocelli (Fig. 53). Face with supraclypeal region finely strigose, otherwise with distinctive mesh-like sculpture, the sculpture narrowed toward midline so as to more or less form a median carina (Fig. 52). Eye moderately large, with about 20–25 ommatidia in female and 30–35 ommatidia in male; separated from oral margin by distinct malar space of similar

width as mandible (Figs 52, 54). Antenna of female as in Fig. 172.

Mesosoma with propleura completely divided medially (Fig. 112). Forewing as in Fig. 165, with 43–48 very long and thin (hair-like), evenly spaced marginal setae over about apical half of wing, 12–15 much shorter setae basally along anterior margin, and with 6 or 7 variably shorter setae basally along posterior margin, of which at least the basal 3 setae are comparatively long and at least the distal seta (sometimes distal 1–3 setae) are quite short. Metanotum separated from metapleuron laterally and from propodeum posterolaterally (Figs 105, 106).

Metasoma of male without seta on Mt<sub>7</sub> (Fig. 155).

*Remarks*.—Body length varies from about 0.5 mm in air-dried individuals to about 0.7 mm in some critical-point dried females. The difference appears to be mostly because the gaster remains inflated in critical-point dried specimens. Females with the gaster neither shrunken nor obviously over-inflated are about 0.65 mm. The species description of *Z. valentinei* is brief because it mostly includes only those features that readily differentiate it from *Z. insulare*.

## SUPRAFAMILIAL RELATIONSHIPS

One of the objectives of this study was to determine whether any additional morphological evidence could be found to help resolve the suprafamilial relationships of Mymarommatoidea. Mymarommatoidea has been proposed as the sister group of either Serphitoidea (Kozlov and Rasnitsyn 1979) or Chalcidoidea (Gibson 1986). We therefore included fossils of Serphitidae in our study, but our observations are based on only seven Taimyr and nine Canadian Cretaceous specimens. Our study of mymarommatoidea revealed that they are much more diverse morphologically than thought previously. Consequently, the inferences made below should all be considered as tentative until character-state dis-

tribution and groundplan features of Serphitidae are determined more accurately through an equally comprehensive study.

A Mymarommatoidea + Serphitoidea sister-group relationship is supported by common possession of a similarly structured 2-segmented petiole (Kozlov and Rasnitsyn 1979), whereas common possession of axillar phragmata as the sites of origin for tubular mesotergal-mesotrochanteral muscles is the principal evidence for a Mymarommatoidea + Chalcidoidea relationship (Gibson 1986). Vilhelmsen and Krogmann (2006, figs 12–14) showed that the prophragma of *M. anomalum* has rod-like structures similar to axillar phragmata. They suggested that this apparent “serial” homology and the different structure of the axillar phragmata in mymarommatids and chalcids (tubular *vs.* flat) might indicate that the phragmata evolved independently in the two taxa. However, Mymarommatoidea and Chalcidoidea are still the only known apocritans having the mesotrochanteral depressor muscle consisting only of a notal portion that originates at least partly from an axillar phragma. Our study shows that Cretaceous mymarommatids also had tubular mesotrochanteral depressor muscles originating from rod-like axillar phragmata (Fig. 206: axp). Knowledge of the structure of this muscle in Serphitidae would therefore be valuable for inferring relationships. Serphitids are much more highly sclerotized and melanized than are mymarommatids and we did not see any specimen in which the internal musculature was visible.

As noted by Vilhelmsen and Krogmann (2006), the presence or absence of an exposed prepectus and the position of the mesothoracic spiracle are other phylogenetically informative features for inferring relationships of Chalcidoidea. The position of the mesothoracic spiracle in Chalcidoidea is autapomorphic, being at or above the dorsal margin of the prepectus between the pronotum and mesoscutum (Gibson 1986, figs 18–29). Other parasitic Hyme-

noptera have the spiracle ventral to the level of the dorsal margin of the pronotum, either between the pronotum and mesopleuron or secondarily on the pronotum in the same relative position. Furthermore, the prepectus or its remnant extends dorsally behind the spiracle, between it and the mesopleuron (Gibson 1985, figs 19–26), except in Stephanidae (Gibson 1985, fig. 16) and Ichneumonoidea (Gibson 1985, figs 27, 28). Although a pronotal notch was not observed in any fossil mymarommatoid or in *Zealaromma* (Figs 103, 108), the incision on the posterior margin of the pronotum of some mymarommatids (Figs 16, 82: pn; 99, 101) could indicate the position of the mesothoracic spiracle before it was lost. If so, the ancestor of mymarommatoids had the mesothoracic spiracle in the sympleosomorphic position for parasitic Hymenoptera. It therefore is not useful for establishing relationships of Mymarommatoidea, but supports the hypothesis of autapomorphy for Chalcidoidea.

In lateral view, one specimen of Serphitidae from Taimyr amber (PIN: 3730/31) very clearly has a white, globular mesothoracic spiracle ventral to the dorsal margin of the pronotum between the pronotum and mesopleuron (Figs 220, 221: sp). The spiracle appears to lie partly within the excised posterodorsal margin of the pronotum (most clearly visible from a somewhat ventral view, Fig. 222: sp). In lateral (Figs 220, 221) or ventrolateral (Fig. 222) view, about the dorsal third of the posterior margin of the pronotum abuts the anterior margin of the mesopleuron, but ventrally a slender, spindle-shaped region (Figs 220–222: pre?) separates the posterior margin of the pronotum from the mesopleuron between the spiracle and procoxa. This intervening region appears to be a separate sclerite because its anterior margin is delimited by a distinct suture and it is on a lower level than the posterior margin of the pronotum, because it is separated from the mesopectus by a distinct

suture at least ventrally, and because its sculpture is different from the putative pronotum and mesopectus (with longitudinal rugae compared to rugose pronotum and mesopectus). The region could be a differentiated part of the mesopectus, but more likely it is a relatively long and slender prepectus. In lateral view, the mesothoracic spiracle extends over the anterior margin of the mesopleuron (Figs 220–222) and appears to be on a slightly higher level than the mesopleuron. This is because the mesopleuron posterior to the spiracle is slightly concave. The concave region is distinct because it is delineated by carinae (Fig. 221: c). Many extant platygastroid (Gibson 1985, figs 23, 24) and some proctotrupoid (Gibson 1985, figs 19a, 20a, 25a) taxa also have the spiracle on a slightly higher level than the mesopleuron because the posterior pronotal inflection extends dorsally under and behind the spiracle. This suggests that if the slender region of PIN: 3730/31 is the prepectus then it likely also extends dorsally behind the spiracle. If so, the prepectal structure is more similar to that of Monomachidae (Gibson 1985, fig. 15) than Stephanidae (Gibson 1985, fig. 16). Because of the intervening region, the posterior margin of the pronotum is somewhat sinuate (Figs 220–222). The posterior margin of the pronotum is similarly sinuate in many Scelionidae (Platygastroidea) having a netrion (Gibson 1985, fig. 23). Rasnitsyn (1980) hypothesized that the netrion in scelionids is the prepectus fused with the pronotum. The similarity between the putative sclerite of PIN: 3730/31 and the netrion of some scelionids suggests that it might be fused with the pronotum internal to the external suture (*cf.* Figs 220–222 with Gibson 1985, fig. 23 and Masner 1979, figs 4–8). If so, it is structurally the same as a netrion and therefore a possible synapomorphy for Serphitoidea + Platygastroidea.

The other serphitids we examined did not have such a distinctly differentiated

mesopectal region, though the specimen in PIN: 3311/80 and the largest of the three specimens in PIN: 3730/28–30 has an obscurely differentiated region between the pronotum and mesopectus, at least on the right side from direct ventral view. The region is less distinct in these two specimens partly because it is quite smooth, similar in sculpture to the pronotum and mesopleuron. The posterior margin of the pronotum of the holotype of *Microserphites parvulus* Kozlov and Rasnitsyn was also stated as having a narrow border (Kozlov and Rasnitsyn 1979, fig. 7), which may be equivalent to the region we observed in PIN: 3730/31. Further study is necessary to determine whether all Serphitidae have a slender mesopectal region differentiated below the mesothoracic spiracle, whether this region is a free prepectus or a netrion, and whether the posterior margin of the pronotum is free from the mesopleuron or connected by a posterior pronotal inflection. These observations could be complicated because the pronotum is somewhat moveable relative to the mesothorax in extant apocritans with a prepectus (e.g. Monomachidae). The pronotum could overlie and partly or entirely conceal the sclerite in some fossils if the slender region in PIN: 3730/31 is a free prepectus rather than a fused netrion. The margin of the sclerite adjacent to the pronotum appears to be on a slightly lower level than the pronotum in PIN: 3730/31, which suggests that the pronotum can override the sclerite. Study of other individuals of the same species as in PIN: 3730/31 could help determine whether the pronotum is moveable, and therefore whether the sclerite is more likely a prepectus or a netrion. The species is readily identified by the presence of a distinct setal patch on the mesopectus near the procoxa (Figs 220, 222: sep).

Rasnitsyn et al. (2004, p. 128) stated that “monophyly of Khutelchalcididae within Chalcidoidea is very likely” based on presence of a spiracular excision in the pronotum (as an indicator of the chalcid

synapomorphy of a dorsal spiracular position) and a free prepectus. However, if their interpretation of the unique fossil comprising the family is correct, then the comparatively large incision in the postero-dorsal margin of the pronotum (Rasnitsyn et al. 2004, fig. 6) shows that the spiracle is in the symplesiomorphic position relative to chalcids. This placement of the putative spiracle and the vertical structure ventral to it, which they interpret as the prepectus (Rasnitsyn et al. 2004, fig. 6), resemble the structure of the serphitid (Fig. 222) in PIN: 3730/31. As noted above, the presence of a free prepectus is symplesiomorphic and does not support monophyly of Khutelchalcididae + Chalcidoidea. The thoracic structure of Monomachidae, Serphitidae, Khutelchalcididae and some Aculeata suggest that one or more early lineages of Apocrita had a free prepectus that was visible ventral to the spiracle depending on position of a somewhat mobile pronotum. The ancestor of Platygastroidea may have had a similar structure, but it is only in Chalcidoidea that the prepectus was enlarged secondarily to intervene between the pronotum and mesopleuron dorsally. This prepectal structure apparently was derived concurrently with the dorsal shift in position of the mesothoracic spiracle. Of critical importance in taxa with a prepectus, whether this is free or secondarily fused with the pronotum, is whether it extends behind and above the level of the mesothoracic spiracle. Unfortunately, this can usually be determined only by dissecting the pronotum from the mesothorax and therefore is not readily apparent in fossils. However, the exact structure of the prepectus/netrion in Serphitidae may be determined if a fossil is discovered with the pronotum or prothorax detached from the mesothorax.

Mymarommatoidea, Serphitoidea, Platygastroidea and most parasitic Hymenoptera other than Chalcidoidea have a more or less gibbous mesoscutum and the pronotum triangular in lateral view (Gib-

son 1985, figs 21, 23, 27, 29). These features are not evidence of relationships. Gibson (1986) showed that structure of the pronotum and mesonotum is correlated with presence or absence of a free prepectus and relative mobility of the pronotum. Examination of the serphitids we could observe in ventral view shows a propleural structure (Fig. 222: ppm) very similar to extant mymarommatoids with the propleura abutting along their entire length (Fig. 112). Vilhelmsen and Krogmann (2006) correctly stated that most Chalcidoidea have the prosternum partly exposed because the ventral margins of the propleura are more or less divergent. Mymarommatoids are therefore more similar to serphitids than to chalcids in their propleural structure. However, this structure is shared with most Hymenoptera excluding Chalcidoidea and the most basal symphytan lineages (Vilhelmsen and Krogmann 2006). The basal symphytan lineages with chalcid-like propleura also have the pronotum comparatively mobile relative to the mesothorax. Further study is required to determine whether there is a correlation between propleural structure and pronotal mobility similar to that of the pronotal-mesonotal complex. Such a study should include Aculeata with an independent prepectus and a relatively mobile pronotum as well as aculeates with a rigidly attached pronotum.

Most apocritans have a curved, apically bifurcate protibial calcar (Basibuyuk and Quicke 1995). Only Chalcidoidea and Mymarommatoidea have some members with this calcar structure and others with a short, straight, needle-like calcar. Because Chalcidoidea and Mymarommatoidea are both well substantiated as monophyletic taxa, the reduced calcar shared by some members of both groups must be convergent. For the same reason, the similar forewing and hind wing structures of mymarommatoids and most *Mymar* (cf. Figs 1–7 with 129–136) are certainly convergent.



Kozlov and Rasnitsyn (1979) did not provide the tibial spur formula for *Microserphites* or *Aposerphites* Kozlov and Rasnitsyn, but stated that this was 1:2:2 for *Serphites* Brues. Most of the serphitids we examined had two distinct meso- and metatibial spurs, though these were not visible in all examined inclusions. Naumann and Masner (1985) listed the tibial spur formula as 1:2:2 for 9 of the 11 families they treated as the "proctotrupoid complex" of families. The formula was listed as 1:2:2 or 1:1:1 for Scelionidae and Platygasteridae, but Austin and Field (1997) stated that members of the most primitive tribes of Platygastroidea are plesiomorphic in having two mesotibial spurs. The number of mesotibial spurs is also variable in Ceraphronoidea. Members of Megaspilidae have two and members of Ceraphronidae one mesotibial spur (Gauld and Bolton 1988). We found that the tibial spur formula is 1:0:2 for Stephanidae and 1:1:2 for Megalyridae and most Chalcidoidea. A few Chalcidoidea only have a single metatibial spur, but the exceptions include some of the tiniest Mymaridae, such as species of *Alaptus* Westwood and *Camptoptera* Förster. At least extant mymarommatids lack both meso- and metatibial spurs, though the tibiae have socketed setae ventroapically (pseudospurs) that can be mistaken for tibial spurs (Figs 139b, c; 141b, c; 144b, c: ps). Absence of meso- and metatibial spurs from mymarommatids and the loss of one mesotibial spur from more derived Platygastroidea and in Ceraphronidae might be correlated with very small body size. If so, the presence of only a single mesotibial spur in Chalcidoidea could indicate that their common ancestor was very small. This would support the hypothesis that the chalcid ancestor was an egg parasitoid rather than a parasitoid of a wood-boring insect (Gibson et al. 1999). However, even though most Cynipoidea have two mesotibial spurs, some species of *Ibalia* Latreille (Ibaliidae) have only a single mesotibial spur (Ronquist and Nordlander

1989, Liu and Nordlander 1992). This, along with loss of one mesotibial spur from Megalyridae and both mesotibial spurs from Stephanidae, suggests that there could be some correlation between parasitism of wood-boring insects and the loss of mesotibial spurs. The single mesotibial spur shared by Chalcidoidea and Megalyridae presumably is convergent, but further study of the number of mesotibial spurs throughout Apocrita is warranted for phylogenetic inference.

The similar forewing venation of most Chalcidoidea and Scelionidae has often been cited as possibly indicating a sister-group relationship between Chalcidoidea and Platygastroidea. The venation is reduced to single vein complex near the anterior margin of the wing in most members of both groups. Typically, there is a "submarginal", "marginal", "stigmal" and "postmarginal" vein, and often also a short "uncus" projecting from the stigmal vein (Huber and Sharkey 1993, fig. 14; Gibson 1997, fig. 5). Rasnitsyn et al. (2004) stated that the forewing pterostigma was not prominent and possibly was absent from Khutelchalcididae, unlike in an undescribed fossil they identified as a scelionid from the lowermost Cretaceous. The photograph of this putative scelionid shows a costal vein (Rasnitsyn et al. 2004, fig. 7: c) and a longitudinal pterostigma distal to a "pre-pterostigmal break", plus an oblique r-rs (= stigmal vein) projecting from the pterostigma near its middle. Another photograph of the same impression sent to us by Alex Rasnitsyn (PIN) more clearly shows the venation (Fig. 227). The presence of a pterostigma suggests that the marginal vein of extant scelionids evolved through a gradual narrowing of the pterostigma into an only somewhat thickened vein-like structure (A. Rasnitsyn, pers. comm.). However, the groundplan venation of extant Platygastroidea is controversial. Masner et al. (in press) reinterpreted the groundplan forewing venation of Scelionidae based on the putative basal

extant lineages of the group. They noted that members of these lineages lack a marginal vein. Rather, the submarginal vein (R) bifurcates distally before attaining the anterior margin of the wing so that the stigmal vein (r-rs) originates within the membrane and is separated from the wing margin by a short  $R_1$  (Masner et al. in press, figs 41–43, 45–47). Based on this, they concluded that a marginal vein evolved secondarily in Scelionidae and is convergent with the marginal vein of Chalcidoidea. They did not state explicitly how the marginal vein of some scelionids evolved, but they illustrated a distal extension of  $R_1$  along the wing margin in some scelionids as producing the postmarginal vein (Masner et al. in press, figs 46, 47). Presumably, secondary proximal lengthening of R along the wing margin resulted in the marginal vein of some scelionids (Masner et al. in press, fig. 44).

Masner et al. (in press, fig. 49) compared their interpretation of the groundplan venation of Platygastroidea with Cynipoidea to illustrate presumed symplesiomorphic features. The groundplan venation of Platygastroidea, as interpreted from basal extant lineages, can also be derived readily from the venation characteristic of Serphitidae. Kozlov and Rasnitsyn (1979, fig. 2; Rasnitsyn et al. 2004, fig. 8) described and illustrated a costal vein and a distinct pterostigma in *Serphites*, but indicated that the costal vein was missing and the pterostigma was indistinct in *Microserphites parvulus* (Kozlov and Rasnitsyn 1979, fig. 6). A specimen of *Serphites* from Canadian Cretaceous amber (MCZ: 5330) has a distinct pterostigma but lacks a costal vein. Vein R bifurcates before the anterior margin of the wing so that  $R_1$  constitutes the anterobasal and anterior margins of the pterostigma and r-rs constitutes the posterior margin of the pterostigma (Fig. 226). Except for the pterostigma, this venation is very similar to the possible groundplan venation of Platygas-

troidea. However, the unusually large “pterostigma” of serphitids may be because of autapomorphic secondary melanization of the wing membrane in the region between  $R_1$  and r-rs (Fig. 226).

The precursor of the marginal vein of Chalcidoidea is uncertain. The chalcid marginal vein may have evolved through a narrowing of a pterostigma in a transformation similar to that proposed for Scelionidae by A. Rasnitsyn. Alternatively, it may have evolved through anterior elongation of vein R along the wing margin similar to the transformation series proposed for Scelionidae by Masner et al. (in press). If the latter, the marginal vein of chalcids consists only of R, not C+R (Huber and Sharkey 1993, fig. 14; Masner et al. in press, fig. 48) or  $Sc_2+R_1$  (Bradley 1955) or  $R_1$  (Burks 1938). Regardless of the correct interpretation of the groundplan venation of extant Platygastroidea, both hypotheses suggest that the marginal vein of Scelionidae is secondarily derived and therefore convergent to that of Chalcidoidea. Mymarommatoidea also have a recognizable marginal vein (Figs 127, 129, 185: mv) that appears to have a very short stigmal vein distally (Fig. 185: stv). These features may be synapomorphic for Mymarommatoidea + Chalcidoidea, but if so they are homoplastic relative to the venation of some Platygastroidea.

The presence of a costal vein in some fossils assigned to Scelionidae (Fig. 227: cv) and the lack of a costal vein in some Serphitidae (Fig. 226) indicates that loss of this vein occurred independently in the two taxa. Both taxa are known from the earliest Cretaceous or latest Jurassic (Rasnitsyn et al. 2004) so perhaps it is unremarkable that both families exhibit a diversity of wing venation. However, the earliest fossil “scelionids” are impression fossils, from which far less morphological information can be deduced than from amber fossils. The putative scelionids with a pterostigma and a costal vein may only resemble and not actually be closely

related to extant Scelionidae. Further research is necessary to establish this and to resolve the true groundplan venation of extant Scelionidae.

Further study of the external and internal structure of the different types of claval sensilla of mymarommatids and other apocritans is also required. Mymaridae (Figs 8–10: s4) have sensilla that in external structure are very similar to the s4-type sensilla of mymarommatids (Figs 58, 60, 62–64, 66, 68, 70, 71: s4). In Mymaridae they have been called “basiconic” (Baaren et al. 1999, figs 2F, 4A, 4B, 4F, 5F), “grooved peg” (Chiappini et al. 2001, figs 1a, 1c, 16) or “sickle-shaped” (Huber and Fidalgo 1997, figs 47, 48) sensilla. Chiappini et al. (2001) stated that the clava of *Anagrus atomus* (L.) (Mymaridae) has a single such sensillum near its ventral margin almost at its middle, and 1–3 sensilla distally on the apical three (of five) funicular segments. Baaren et al. (1999) reported that in *Anaphes listronoti* Huber and *Anaphes victus* Huber (Mymaridae) all but the first of six funicular segments have one or two of the sensilla distally and both claval segments each have two sensilla. There is at least one s4-type sensilla ventroapically on the female clava of *Polynema striaticorne* Girault (Mymaridae) (Isidoro et al. 1996, fig. 8c). Consequently, mymarids appear to differ from mymarommatids in having the sensilla not only on the clava but also distally on some funicular segments (Figs 9, 10: s4) in a position similar to those of the claval segments of male mymarommatids (cf. Figs 60, 61, 66, 68). Female mymarids have the sensilla ventrally (Fig. 8), dorsally (Fig. 9) or both ventrally and dorsally (Huber and Fidalgo 1997, fig. 48), and in some specimens they can be present on a segment of one antenna but missing from the same segment of the other antenna (Huber and Fidalgo 1997). In addition to mymarids and mymarommatids, individuals of both described genera of Rotoitidae (Chalcidoidea) have apically projecting,

lanceolate sensilla originating from a depression distally on the claval and funicular segments (Figs 75–77), and according to John Heraty (UCRC, pers. comm.) they are also present in some Aphelinidae (e.g. *Cales* Howard). We are not aware of any reports of similarly shaped sensilla in other Chalcidoidea, although so called basiconic, campaniform, capitate peg or multiporous grooved sensilla reported in Agaonidae (Ware and Compton 1992, fig. 3), Eulophidae (Veen and Wijk 1985, fig. 9c), Encyrtidae (Baaren et al. 1996, figs 1, 5f), Pteromalidae (Miller 1972, figs 3, 4), and Trichogrammatidae (Voegelé et al. 1975, pl. III figs 1–4; Olson and Andow 1993, figs 1, 11) likely are homologous with s4-type sensilla. Even though they have a different external structure, they all originate from a circular depression and usually at least some are positioned distally on the funicular segments similar to s4-type sensilla in mymarids and mymarommatids. A reduction in the length and globular enlargement of the apex of a lanceolate s4-type mymarid or mymarommatid sensillum would result in a petiolate, mushroom-like sensillum similar to those of the other chalcid families listed above. The presence of lanceolate s4-type sensilla in Mymaridae and Rotoitidae suggest that these are groundplan features of Chalcidoidea, but that the shape of the sensillum likely was modified secondarily in other chalcids. Chiappini et al. (2001, figs 1c, 18) called a small peg-like sensillum that is ventroapical in position on the clava of *Anagrus atomus* (cf. Fig. 8: s4?) a “sunken peg sensillum”. Our very limited survey of the sensilla in Mymaridae suggests that the sunken peg sensillum in *A. atomus* may be nothing more than a modified s4-type sensillum (cf. Figs 8, 9). More comprehensive surveys are required to determine the exact distribution of lanceolate s4-type sensilla in Chalcidoidea, whether such sensilla occur in other apocritan groups, and whether it is possible to demonstrate structural transformation series from

which phylogenetic inferences can be made.

Further study of the different types of dorsal (s2-type) and ventral (s3-type) claval sensilla are also warranted for phylogenetic inference. Mymarid females have a row or rows of specialized trichoid sensilla along the ventral surface of the clava (Fig. 9: s3), which Baaren et al. (1999) called "sensilla chaetica". These sensilla are similar to the s3-type sensilla of mymaromatoids (Figs 64: s3; 181b). Baaren et al. (1999) described four different types of sensilla chaetica in *Anaphes listronoti*, including an apical sensillum (their type 1), which at least some female mymaromatids have (cf. Figs 8, 9 with Fig. 64: as; 67, 69). They also differentiated three other morphological types of ventral sensilla chaetica. Isidoro et al. (1996, fig 8d) suggested that a double row of robust sensilla ventrally on the clava of female *P. striaticorne* are multiporous gustatory sensilla. Although we did not study the morphology of the ventral row or rows of sensilla in mymaromatids in detail, more than one structure of s3-type sensilla is evident for at least some species (Fig. 72, insert).

Barlin (1978) proposed that the uniquely structured multiporous plate sensilla (mps) of Chalcidoidea evolved from bent multiporous setiform (s2-type) sensilla that became attached to the cuticle. The pore-canal opening in the proximal end of the mps and the unattached distal end of the mps were cited as possible evidence. Kozlov and Rasnitsyn (1979) further suggested that the thick, basally curved sensilla on the clava of female mymaromatids (Figs 63, 64: s2) might be precursors of the mps of Chalcidoidea (Figs 9, 10: mps). They also proposed that the latter evolved through accretion of the ventral surface of the sensillum to the surface of the segment (see also, Basibuyuk and Quicke 1999). Our study supports such an "accretion" hypothesis for the origin of the unique, chalcid-like mps (Gibson 1986 fig. 4; Basi-

buyuk and Quicke 1999, fig. 5d). However, parasitic Hymenoptera other than Mymarommatidae also have long, thick, basally bent sensilla. Basibuyuk and Quicke (1999) stated that Ceraphronoidea, Platygastroidea (Isidoro et al. 1996, fig. 2) and some Proctotrupeoidea, particularly Diapriidae (Basibuyuk and Quicke 1999, fig. 5a), have distinctive, curved, multiporous setiform sensilla. Maamingidae also have such sensilla, each recessed into a shallow longitudinal groove (Early et al. 2001) and with the apices of some of the sensilla extending beyond the apex of the segment (Fig. 74). Fusion of the lower surface of the sensillum within the longitudinal groove would result in a mps external structure very similar to that characteristic of chalcids (cf. Figs 74, 77). As noted by Basibuyuk and Quicke (1999, p. 53), mps vary in shape, but are "always embedded in a chamber in the antennal integument".

A comprehensive survey of the mps structure of chalcids is required to determine their diversity more accurately, but the mps of Mymaridae appear to be quite typical for Chalcidoidea. The mps are structurally diverse in Rotoitidae. Those of *R. basalis* (Fig. 76) are somewhat intermediate between a typical chalcid-like mps and a s2-type sensillum. The sensilla are non-socketed, as for chalcid mps, but they resemble a very thick s2-type sensillum because only the oval base is confluent with the surface and the longer and more slender curved portion, rather than just the apex, is free above the surface. Furthermore, under higher magnification there is a fine groove around the base of the sensillum (Fig. 76) reminiscent of a socket. The mps of *Chiloe micropteron* Gibson and Huber (Fig. 75) are more similar to typical chalcid-like mps. An undescribed species of *Rotoita* near *R. basalis* also has chalcid-like mps, except that on the funicular segments at least some of the convex mps have a distinct groove on either side (Fig. 77), and on the clava the mps originate more distinctly within a longitudinal

depression. Both the funicular and claval segments of the undescribed *Rotoita* also have much more slender, curved sensilla that resemble s2-type sensilla except that they are non-socketed (Fig. 77: s2/mps). Kozlov and Rasnitsyn (1979) partly differentiated serphitids from mymarommatids based on the absence of strong, curved sensilla from the clava of serphitids. The serphitids we examined also lacked s2-type sensilla. The flagellar segments of serphitids (Figs 218, 219) appear to be more or less uniformly covered with suberect, curved, trichoid sensilla, though these could be multiporous setiform sensilla.

Even if chalcid mps were derived from s2-type sensilla, the wide distribution of s2-type sensilla in parasitic Hymenoptera indicates their presence is synapomorphic for a larger group of taxa than just Mymarommatoidea + Chalcidoidea. In Chalcidoidea, both sexes have mps and they are on the funicular as well as the claval segments. Therefore, their immediate common ancestor may also have had s2-type sensilla in both sexes on all the flagellar segments, unlike Mymarommatidae. Rasnitsyn et al. (2004, fig. 5) suggested that lines on the flagellar segments of Khutelchalcididae were internal apertures of long mps and that these were a synapomorphy for Khutelchalcididae + Chalcidoidea. It is also possible that the lines are remnants of elongate s2-type sensilla similar to those in Maamingidae (Fig. 74). According to Barlin (1978), the internal aperture extends the length of the mps in Chalcidoidea and in some subfamilies of Braconidae (Ichneumonoidea). Cynipoidea also have elongate mps, but with long internal apertures only in Cynipidae (Rasnitsyn et al. 2004). According to Barlin (1978), the pore canal for entry of the dendrites occurs at the proximal end of the sensillum in Chalcidoidea but near the center of the sensillum in Cynipoidea and Ichneumonoidea. Although the irregular lines on the flagellar segments of Khutelchalcididae might be elongate internal

apertures of mps, they do not show the unique features of chalcid mps — internally, the proximal position of the pore canal and, externally, the sensillum being raised, ridge-like, above the surface of the cuticle, without an encircling groove, and with the distal end free (Basibuyuk and Quicke 1999, fig. 5d). Additional study is necessary to confirm the presence of mps in other fossil impressions of Khutelchalcididae, to determine the internal structure of the mps in Rotoitidae, and to assess more thoroughly the internal and external structure of the flagellar sensilla throughout parasitic Hymenoptera. A comprehensive survey of the setation/sensilla of the metanotum and around the wing bases throughout parasitic Hymenoptera might also provide additional characters and transformation series for phylogenetic inference.

Except for Serphitidae, mymarommatids are unique in having the second metasomal segment tubular (Figs 88, 89). The functional or ecological significance of a tubular second metasomal segment is unknown. The post-petiolar metasoma (gaster) of Mymarommatoidea is quite similar to that of Chalcidoidea. Similarities include cerci on the syntergum and absence of spiracles from all but the penultimate tergite in the groundplan of Mymarommatoidea, tergites smoothly overlapping the sternites, the hypopygium being able to separate widely from the syntergum in females, and an ovipositor that rotates and extends ventrally from the gaster rather than being extended posteriorly. However, all of these features have a much wider distribution in Apocrita and at best support the monophyly of a much larger group of taxa than just Mymarommatoidea + Chalcidoidea.

Kozlov and Rasnitsyn (1979) stated that the gastral tergites protrude laterally somewhat and the sternites form a longitudinal fold in *Microserphites*. A serphitid in Canadian Cretaceous amber (MCZ: 5343) has what we interpret as a similar gastral structure. This specimen belongs to

*Serphites* based on its wing venation and position of the posterior ocellus. In ventral view, the gaster is strongly flattened with the ventrolateral aspect of each tergite extending on either side of the sternum for a short distance before being abruptly angled back toward the sternum. Consequently, the gaster is uniformly carinately margined laterally and ventrally has distinctly differentiated "laterotergites" forming a narrow band on either side of the sternum (*cf.* Fig. 224: ltt). The abruptly folded tergal structure is most distinct for the basal gastral tergites because both the dorsal and ventral surfaces are visible, but it is not possible to determine whether the laterotergites articulate with differentiated laterosternites. The gastral sternum is composed of six sternites that form a uniformly low convex surface; the second gastral sternite is transverse-rectangular and is the largest sternite, though only slightly longer than the first gastral sternite. Several Taimyr amber serphitids (PIN: 3311/80, PIN: 3730/28-30 (Fig. 224), PIN: 3731) have gastral structures very similar to that described for the MCZ: 5343 specimen. These Taimyr specimens represent a species different from MCZ: 5343 based on a very different length of the second petiolar segment. All the Taimyr amber specimens had been identified as "*Serphites* sp.". Kozlov and Rasnitsyn (1979) did not describe laterally differentiated tergites for *Serphites* or their new genus *Aposerphites*. Some fossils we examined and identify as *Serphites* have the gaster subcircular in cross-section rather than flattened. It usually is not possible to be certain whether the tergites have differentiated laterotergites when the gaster is subcircular. However, one specimen (MCZ: 5256) with an inflated gaster has a whitish line laterally. This line superficially divides the tergites from the sternites, but under some angles of light what appears to be quadrate plates and the true ventral margins of the tergites are visible below the whitish line. Another specimen

(MCZ: 5330) has an inflated gaster with the tergites and sternites separated by a distinct, white, membranous band (Fig. 225). Under some angles of light, the tergites are slightly angled along a straight line so that there is a slender region along the tergum above the narrow membranous band (Fig. 225: ltt), which we consider as a band of differentiated laterotergites. Even less distinct is a slender band laterally along the sternites (Fig. 225: lst) that is similar in width to the putative laterotergites. This region appears to consist of a slightly depressed part of each sternite that the respective laterotergite would override if the gaster was not inflated. Based on serphitids with a flattened gaster and deeply inflexed laterotergites, our assumption is that the differentiated lateral part of the sternites can flex so as to lie over the laterotergites, and thus constitute "laterosternites". Regardless, the membranous band separating the sternites and tergites is straight in MCZ: 5330 (Fig. 225), unlike the irregular line of separation between the tergites and sternites in taxa that lack laterotergites, such as mymaromatids (Fig. 147) and chalcids. The latter two Canadian Cretaceous serphitids (MCZ: 5256 and 5330) suggest that laterotergites are present in serphitids, but that they are not obvious when the gaster is inflated. Observation of a differentiated lateral region on the sternites is only possible when the gaster is inflated and the tergites and sternites are separated.

Austin et al. (2005) stated that monophyly of Platygastroidea is supported by two character systems, gustatory sensilla on the claval segments and structure of the gaster. In Platygastroidea, the gastral tergites and sternites are connected by laterotergites and the spiracles are reduced and non-functional. Vanhorniidae (Proctotrupoidea) also lack gastral spiracles but do not have laterotergites (Naumann and Masner 1985), whereas Ambositrinae (Dipriidae) have spiracles on the penultimate gastral tergite and laterotergites (Masner

1961). Most of the serphitids we examined were inappropriately preserved or positioned to be confident of the presence or absence of spiracles, but under some angles of light MCZ: 5330 has a small, smooth, circular structure laterally on  $Mt_7$ , which led Gibson (1985) to code metasomal spiracles as present in Serphitidae. There also appears to be a circular structure laterally on  $Mt_7$  of PIN: 3730/31 that may be a spiracle, which is in a transversely-oval depression that is margined anteriorly. The hypopygium was extended ventrally in most female serphitids we examined similar to mymarommatids and chalcids. Consequently, if the presence of metasomal spiracles is verified for other serphitids, then their gastral structure is more similar to Ambositrinae (Diapriidae) than Platygastroidea, which have a tubular, telescoping ovipositor extension system. The ambositrine gaster differs by having  $Mt_2$  composed of two or three fused terga (Masner 1993).

Masner et al. (in press) discussed four genera of Scelionidae that apparently lack laterotergites, but at least three of the genera have longitudinal sublateral keels on the tergites. These keels may represent vestiges of the lateral fold that differentiates the laterotergites of other platygastroids. Furthermore, the ventral margins of the tergites and the dorsal margins of the sternites form straight lines (Masner et al. in press, fig. 3), which are separated by membrane when the gaster is inflated (Masner et al. in press, fig. 1). This "multi-segmented carapace" structure is very similar to that of other platygastroids with laterotergites and of the MCZ: 5330 serphitid (Fig. 225). Relationships of the four scelionid genera that apparently lack laterotergites need to be clarified because they are all characterized by a single mesotibial spur rather than the groundplan two mesotibial spurs (see above).

The MCZ: 5343 serphitid is a male. The metasoma in ventral view has symmetrical, elongate-digitiform processes that have at

least one long terminal seta (Fig. 223: par?). The processes extend from either side of the sternum at the line of junction between  $Ms_7$  and  $Ms_8$  and in posterior view appear to originate laterally between the apical tergite and sternite. The processes resemble what we consider to be parameres in male *Zealaromma* (Figs 154, 156: par) and *Maa-minga* (Fig. 157: par). Rasnitsyn (1988, node 65) postulated that a tubular male genital capsule with both the volsellae and parameres fused with the aedeagus was synapomorphic for Chalcidoidea + Mymarommatidae + Serphitidae + Platygastroidea and, possibly, the extinct family Jurapriidae. This hypothesis appears to be falsified by the presence of moveable parameres in the male genitalia of *Zealaromma* and, likely, Serphitidae, but the fused condition remains a possible synapomorphy for Chalcidoidea + Platygastroidea.

The metasoma of MCZ: 5343 has seven distinct, melanized tergites in dorsal view and a small, lighter coloured apical eighth tergite that in posterior view originates somewhat under  $Mt_7$ . Laterally on this apical tergite is a circular, somewhat convex structure with several projecting setae, which likely is a cercus. Two females (PIN: 3730/31; MCZ: 5330) also have setose digitiform processes (cf. Gibson 2003, figs 26, 42) basolaterally on  $Mt_8$  that likely are the cerci (Gibson 1985). The left process of PIN: 3730/31 appears to have at least four and probably six projecting setae.

The serphitid head in lateral (Fig. 218) or frontal (Fig. 219) view has the antennae inserted very low on the face close to the oral cavity. In well preserved specimens there is a distinctly differentiated clypeus and the antennal toruli are separated from a linear epistomal suture by a distance similar to the diameter of a torulus. This is typical of the head structure that characterizes Platygastroidea (Naumann and Masner 1985) and contrasts with the higher, possibly plesiomorphic position of the toruli in Mymarommatoida and Chalcidoidea. The mandibles of most serphitids



we examined are quite broad with three long and slender teeth (Fig. 218; Alonso et al. 2000, fig. 2), though the holotype of *Microserphites parvulus* appears to have only two slender teeth (Kozlov and Rasnitsyn 1979, fig. 7). Distinct maxillary and labial palpi are often visible in serphitids, unlike in mymarommatids, though this represents another symplesiomorphy. A feature that may be phylogenetically informative is the presence of an acetabular carina or at least an anteriorly differentiated region of the mesopectus ventrally behind the procoxae (Fig. 220: acc). This carina is absent from mymarommatids (Fig. 86), mymarids and most other chalcids. Although Naumann and Masner (1985) indicated that an acetabular carina was absent in Platygastroidea this was an error — absence or presence of an acetabular carina in Platygastriidae and Scelionidae should have been listed (see Masner 1979).

### CONCLUSIONS

Several structural similarities suggest a close relationship between Serphitoidea and Platygastroidea, though at present there are no unequivocal synapomorphies for the two taxa. Some similarities, such as presence and position of the mesothoracic spiracle and two mesotibial spurs are obvious symplesiomorphies, but other shared features are not studied sufficiently for confident hypotheses of character-state distribution and polarity in Serphitidae or Apocrita. These features include a similarly structured gaster having laterotergites and possibly laterosternites, a differentiated mesopectal region that might be homologous with a netrion or the ancestral structure (prepectus exposed ventral to mesothoracic spiracle) from which a netrion evolved, a forewing venation that could be similar to the groundplan venation of Scelionidae, position of the toruli relative to the epistomal suture, and similar mesosomal sclerotization and sculpture, including an acetabular carina.

Other than the common possession of a 2-segmented petiole, we found no evidence supporting a Serphitoidea + Mymarommatoidea sister-group relationship. The petiolar segments are similar in both taxa, though in some serphitids they are longitudinally strigose and/or extensively setose, unlike the petiolar segments of mymarommatids. Newly discovered similarities, such as medially abutting propleura and independent parameres in the male genitalia have much wider distribution and therefore are indicated as symplesiomorphies.

Common possession of lanceolate s4-type flagellar sensilla and one or two rows of s3-type sensilla ventrally on the clava of females could provide additional support for monophyly of Mymarommatoidea and Chalcidoidea. However, the diverse external and internal structures of different claval and flagellar sensilla found by Isidoro et al. (1996) in parasitic Hymenoptera demonstrate that a much more comprehensive comparative study is required prior to reliable hypotheses. It seems likely that the marginal veins of at least Chalcidoidea and Scelionidae are convergent, though common possession of a marginal vein could be synapomorphic for Mymarommatoidea + Chalcidoidea. Study of the male from lower Cretaceous Spanish amber that Alonso et al. (2000) stated has a 2-segmented petiole but non-mymaromatid wing features, and which they postulated may be the sister taxon of Mymarommatidae + Chalcidoidea (Mymaridae), could provide valuable information for resolving character-transformations and relationships.

The extinct Cretaceous taxon Khutelchalcididae is indicated to be at most the sister-group of Chalcidoidea rather than a "basal chalcidoid". The pronotum has an incision in the posterodorsal margin that suggests the mesothoracic spiracle was in the plesiomorphic position and even though it may have had a slender, externally visible prepectus ventrally, this did not

extend dorsally to the mesoscutum as in Chalcidoidea.

Future studies of higher-level relationships of Chalcidoidea or Mymarommatoidea should include Maamingidae as well as Platygastroidea and Serphitidae as outgroups. Inclusion of Maamingidae is warranted because of the structure of their s2-type antennal sensilla (Fig. 74) compared to the uniquely structured mps of Chalcidoidea, the presence of independent, rod-like parameres in the male genitalia, a forewing venation (Early et al. 2001, fig. 19) similar to that of *Rotoita* (Gibson and Huber 2000, fig. 46), other similarities between the taxa discussed by Early et al. (2001), and relationships indicated by molecular analyses (Castro and Dowton 2006).

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#### Appendix I. Abbreviations used for structures in the illustrations.

acc:	acetabular carina
aea:	aedeagal apodeme
aed:	aedeagus
am:	anterior margin
an:	anus
anp:	anal plate
as:	apical sensillum of clava
asc:	anterior scutellum
xp:	axillar phragma
bc:	basicoxite of metacoxa
c:	carina
ca:	calcar
cc:	costal cell
cer:	cercus
cl:	clava
cl <sub>n</sub> :	claval segment
cs:	campaniform sensillum

ct: coxal trough  
 cv: costal vein  
 cx: coxa  
 d: dorsal mandibular surface  
 dig: digitus  
 dis: digital spine  
 dms: dorsal metapleural sensillum  
 dsc: disc of forewing  
 dt: dorsal tooth of mandible  
 fc: fine comb  
 fs: flagellar setae  
 frp: frontal plate of head capsule  
 fs: flagellar setae  
 fu: funicle  
 fu<sub>n</sub>: funicular segment  
 gp: gonopore  
 ham: hamulus  
 hp: humeral plate  
 hwb: base of hind wing  
 hyp: hypopygium  
 i: inner mandibular surface  
 isp: intersegmental pit  
 lab: labium  
 lbr: labrum  
 lpm: prementum of labium  
 lst: laterosternite  
 ltt: laterotergite  
 max: maxilla  
 mb: membrane  
 mc: macrochaeta of forewing  
 mg: mandibular groove  
 mms: mesopleural-metapleural suture  
 mn: mesopleural notch  
 mnd: mandible  
 mps: multiporous plate sensillum  
 ms: paramedial setae of occipital plate  
 msc: mesoscutum  
 Mt<sub>n</sub>: metasomal tergite  
 mv: marginal vein  
 mxg: galea of maxilla  
 mxp: maxillary palpus  
 mxs: stipes of maxilla  
 no<sub>3</sub>: metanotum  
 o: outer mandibular surface  
 ocp: occipital plate of head capsule  
 op: opposing process of hind wing  
 opp: pit on occipital plate  
 ov: ovipositor  
 ovs: ovipositor sheath  
 paa: parameral apodeme  
 pap: process of labiomaxillary complex  
 par: paramere  
 pas: postalar sensillum  
 pf: propodeal flange  
 pgp: postgenal plate of head capsule  
 pl<sub>3</sub>: metapleuron  
 pl<sub>2</sub>p: mesopleural pit  
 pl<sub>3</sub>p: metapleural pit  
 pn: pronotal notch

ppm: propleural margin  
 pro: propodeum  
 pre: prepectus  
 prs: propodeal seta  
 psc: posterior scutellum  
 ps: pseudospur  
 pss: prespiracular sensillum  
 pst: pterostigma  
 pt<sub>n</sub>: petiolar segment  
 ptp: posterior tentorial pits  
 ret: retinaculum  
 sl-4: type 1, 2, 3 or 4 flagellar sensillum  
 sa: subalar area  
 sas: subalar sensilla of mesopleuron  
 sbt: subbasal tooth  
 sep: setal patch  
 smv: submarginal vein  
 sp: spiracle  
 spa: spiracular aperture  
 spp: spiracular peritreme  
 sps: suprapleural sensillum  
 std: forewing stalk, distal part  
 stk: forewing stalk  
 stp: forewing stalk, proximal part  
 stv: stigmal vein  
 syn: syntergum  
 tg: tegula  
 tra: trachea  
 voa: volsellar apodeme  
 vol: volsella  
 vt: ventral tooth of mandible

## Appendix II. Synopsis of extant material examined.

### *Mymaromma* Blood and Kryger

1. *Mymaromma anomalum* (Blood and Kryger) (numerous individuals, CIRAD, CNC, NHRS, UCRC): **Nearctic** — Canada (ON). **Palaeartic** — Czech Republic, England, France, Germany, Hungary, Italy, Japan, Poland, Russia, Sweden.
2. *Mymaromma buyckxi* Mathot (7♀, 4♂; CNC, ISNB): **Afrotropical** — Congo, Gabon, Madagascar, Nigeria.
3. *Mymaromma goethei* Girault (numerous individuals, ANIC, BPBM, CNC, UCRC): **Australasian** — Australia (QLD, NT, WA), ?Hawaii, Papua New Guinea.
4. *Mymaromma mirissimum* Girault (numerous individuals, ANIC, CNC): **Australasian** — Australia (ACT, QLD, NT, WA), Christmas Island, Norfolk Island.
5. *Mymaromma ypt* (Triapitsyn & Berezovskiy) (33♀, 11♂; CNC, UCRC): **Oriental** — China (Fujian). **Palaeartic** — Russia, South Korea.
6. *Mymaromma* sp. (numerous individuals, CNC, UCRC): **Oriental**: Taiwan, Thailand.

7. *Mymaromma* sp. (numerous individuals, CNC): **Australasian** — Indonesia (Ceram), New Caledonia. **Oriental** — Indonesia (Sulawesi, Sumatra), Malaysia (Sabah), ?Nepal, Philippines (Luzon, Negros), Taiwan, Thailand.
8. *Mymaromma* sp. (3♀, 2♂; CNC, UCRC): **Neotropical** — Bermuda, Colombia, Mexico.
9. *Mymaromma* sp. (1♀, 2♂; CNC): **Neotropical** — Brazil.
10. *Mymaromma* sp. (22♀, 26♂; ANIC, NZAC): **Australasian** — Chatham Island, New Zealand, Norfolk Island.

*Mymaromella* Girault

11. *Mymaromella chaoi* (Lin) (2♀; FAUF): **Oriental** — China.
12. *Mymaromella cyclopterus* (Fidalgo and De Santis) (1♀, MLPA): **Neotropical** — Brazil.
13. *Mymaromella mira* Girault (20♀, 35♂; ANIC, CNC, UCR): **Australasian** — Australia (ACT, SA, WA).
14. *Mymaromella* sp. (43♀, 2♂; CNC, USNM): **Nearctic** — Canada (ON), USA (GA, NC, NY, MD, MI, SC, VA).
15. *Mymaromella* sp. (6♀; CNC): **Nearctic** — Canada (NB, ON, PQ).
16. *Mymaromella* sp. (3♀; CNC, UCRC): **Australasian** — Australia (ACT).
17. *Mymaromella* sp. (11♀; ANIC, BMNH): **Australasian** — Australia (TAS, WA).
18. *Mymaromella* sp. (7♀, 1♂; ANIC, BMNH, UCRC): **Australasian** — Australia (SA, WA).
19. *Mymaromella* sp. (7♀; CNC): **Neotropical** — Brazil, Trinidad, Venezuela.
20. *Mymaromella* sp. (1♀; BMNH): **Afrotropical** — Ivory Coast.
21. *Mymaromella* sp. (6♀; BMNH): **Afrotropical** — Ivory Coast.
22. *Mymaromella* sp. (2♀; CNC): **Palaeartic** — Sweden.
23. *Mymaromella* sp. (1♀; ANIC): **Australasian** — Australia (WA).

*Zealaromma* Gibson, Read and Huber

24. *Zealaromma insulare* (numerous individuals; CNC, NZAC): **Australasian** — New Zealand.
25. *Zealaromma valentinei* (16♀, 5♂; CNC, NZAC): **Australasian** — New Zealand.

Appendix III. Character state summary of  
*Mymarommatoidea*.

1. Head capsule: (0) uniformly sclerotized, a single structure; (1) with a hyperoccipital band of pleated membrane differentiating moveable occipital plate from frontal plate.
2. Mandibular structure: (0) laterally thin, with outer surface convex and apices broadly overlapping when closed; (1) laterally thick, with outer surface convex and apices not meeting when closed (exodont).
3. Number of mandibular teeth: (0) two; (1) three.
4. Paramedial setae on occipital plate: (0) absent; (1) present.
5. Number of supraclypeal interorbital setae: (0) 4; (1) 2.
6. Ocelli: (0) present; (1) absent.
7. Width of labium: (0) about as wide as maxilla; (1) about twice as wide as maxilla.
8. Relative position of maxillary palpus and galea: (0) palpus originating from subapical lobe on inner part of galea; (1) palpus originating apically on lobe ventral to galea.
9. Number of claval segments of female: (0) 4; (1) 3; (2) 2; (3) 1.
10. Structure of multi-segmented clava: (0) segments distinctly separated, forming loosely associated clava; (1) segments compacted, forming tube-like clava.
11. Number of funicular segments of female: (0) 7; (1) 6.
12. Number of s4-type claval sensilla of female: (0) 2; (1) 3.
13. Position of s4-type claval sensilla of female: (0) near dorsal margin; (1) near midline or below.
14. Structure of propleura: (0) abutting, but separated or distinguished medially by distinct line; (1) fused into carapace.
15. Condition of meso- and metapleuron: (0) separated by suture; (1) completely fused or separated by suture only ventrally.
16. Condition of metanotum: (0) independent from metapleuron and propodeum; (1) fused laterally to metapleuron; (2) fused posterolaterally to propodeum; (3) fused to both metapleuron and propodeum.
17. Metapleural pit: (0) present; (1) absent.
18. Position of metapleural pit when present: (0) distinctly nearer spiracle than ventral margin of pleuron; (1) about midway between spiracle and ventral margin of pleuron.
19. Propodeal flange: (0) present laterally as vertical flange but incomplete dorsally; (1) complete laterally and dorsally,  $\cap$ -like.
20. Spiracular peritreme: (0) slit-like; (1) evident only as slender, smooth band of cuticle.
21. Spiracular aperture: (0) circular to oval; (1) elongate, slit-like.
22. Pattern of marginal setae along posterior margin of forewing: (0) with at least three moderately long basal setae; (1) with conspicuously long basal seta proximal to several very short setae; (2) with all setae very short basally.
23. Foretibial calcar: (0) comparatively long, curved and apically bifurcate; (1) comparatively short, straight and simple.

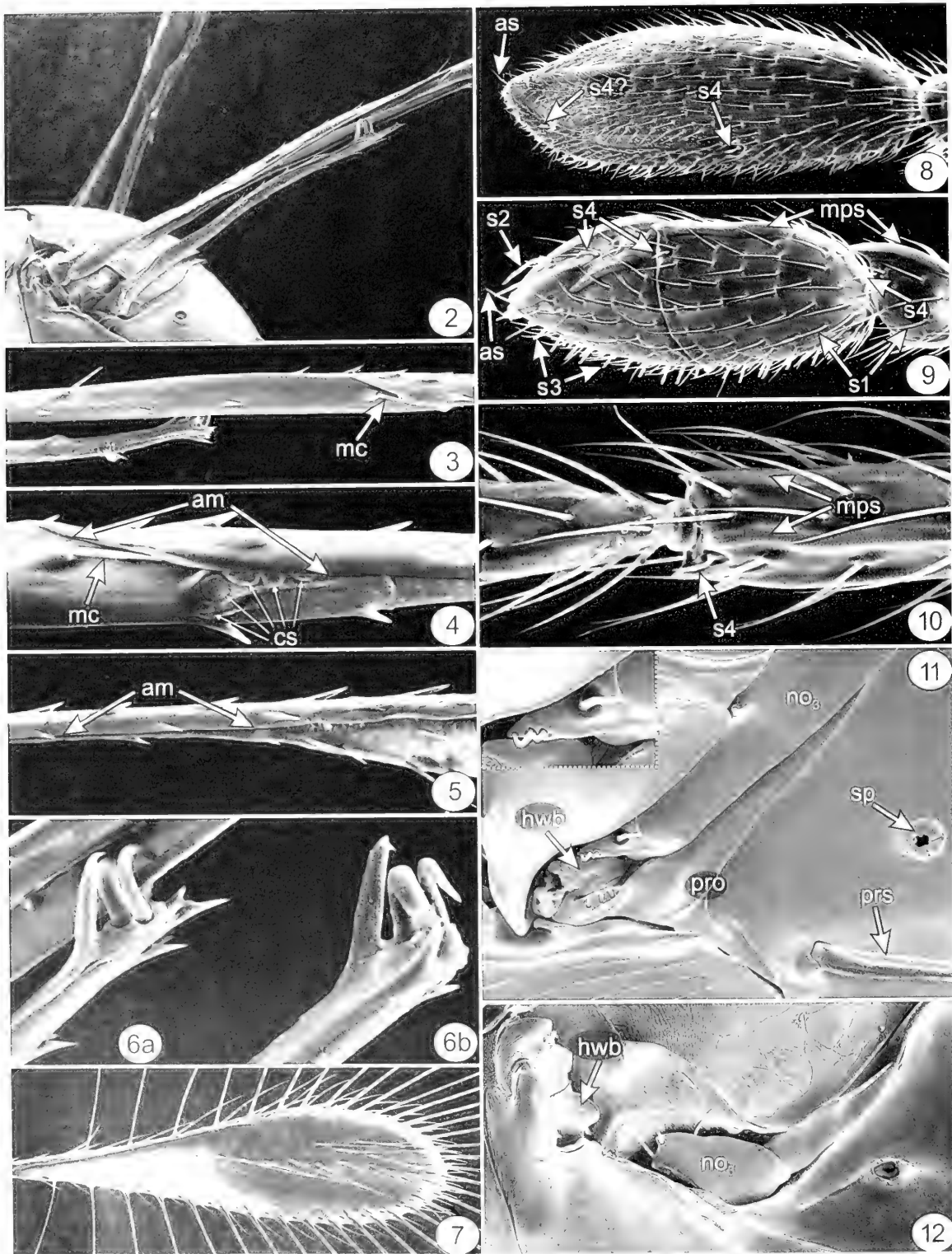


24. Posterior surface of mesofemur: (0) without bumps; (1) with bumps.

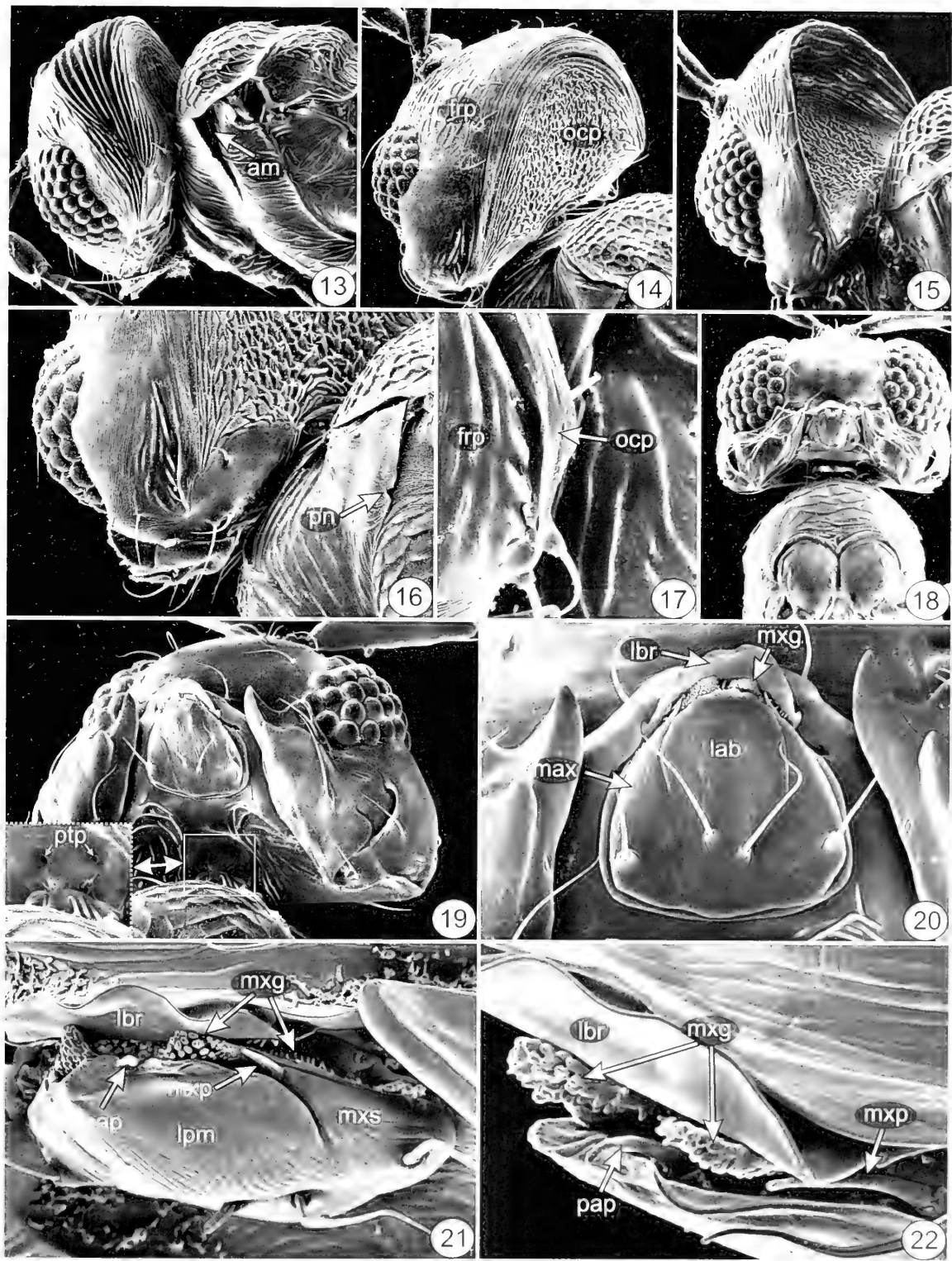
25. Seta laterally on first petiolar segment: (0) present; (1) absent.

26. Metasomal spiracle: (0) present; (1) absent.
27. Cerci: (0) present, though sometimes partly integrated into syntergal surface; (1) absent.

28. Male genitalia: (0) with external parameres; (1) without external parameres.

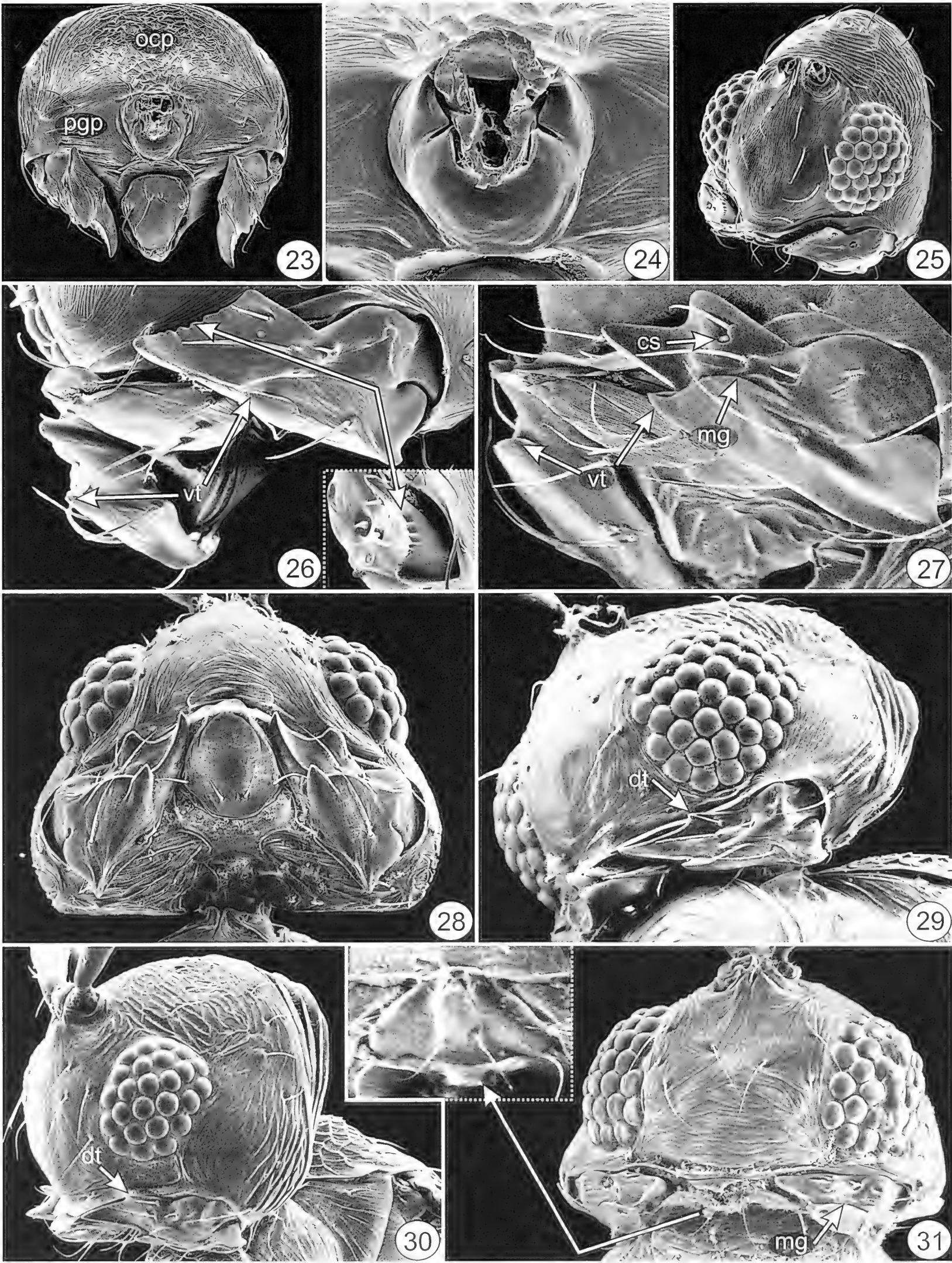


Figs 2-12. 2-7, *Mymar schianni*: 2, forewing stalk and hind wing, ventral; 3, wing coupling, dorsal; 4, forewing stalk sensilla; 5, distal part of forewing stalk; 6, hind wing apex (a: ventral, b: dorsal); 7, forewing disc, dorsal. 8 and 9,  $\gamma$  clava: 8, *Eustochius atripennis*; 9, *M. schianni*. 10, *M. schianni*,  $\gamma$  flagellar segments. 11 and 12, dorsolateral view of metanotum, propodeum and base of hind wing: 11, *Plilomyiinae* sp. (insert: enlargement of lateral metanotal setae); 12, *Mymar laprobancum*.

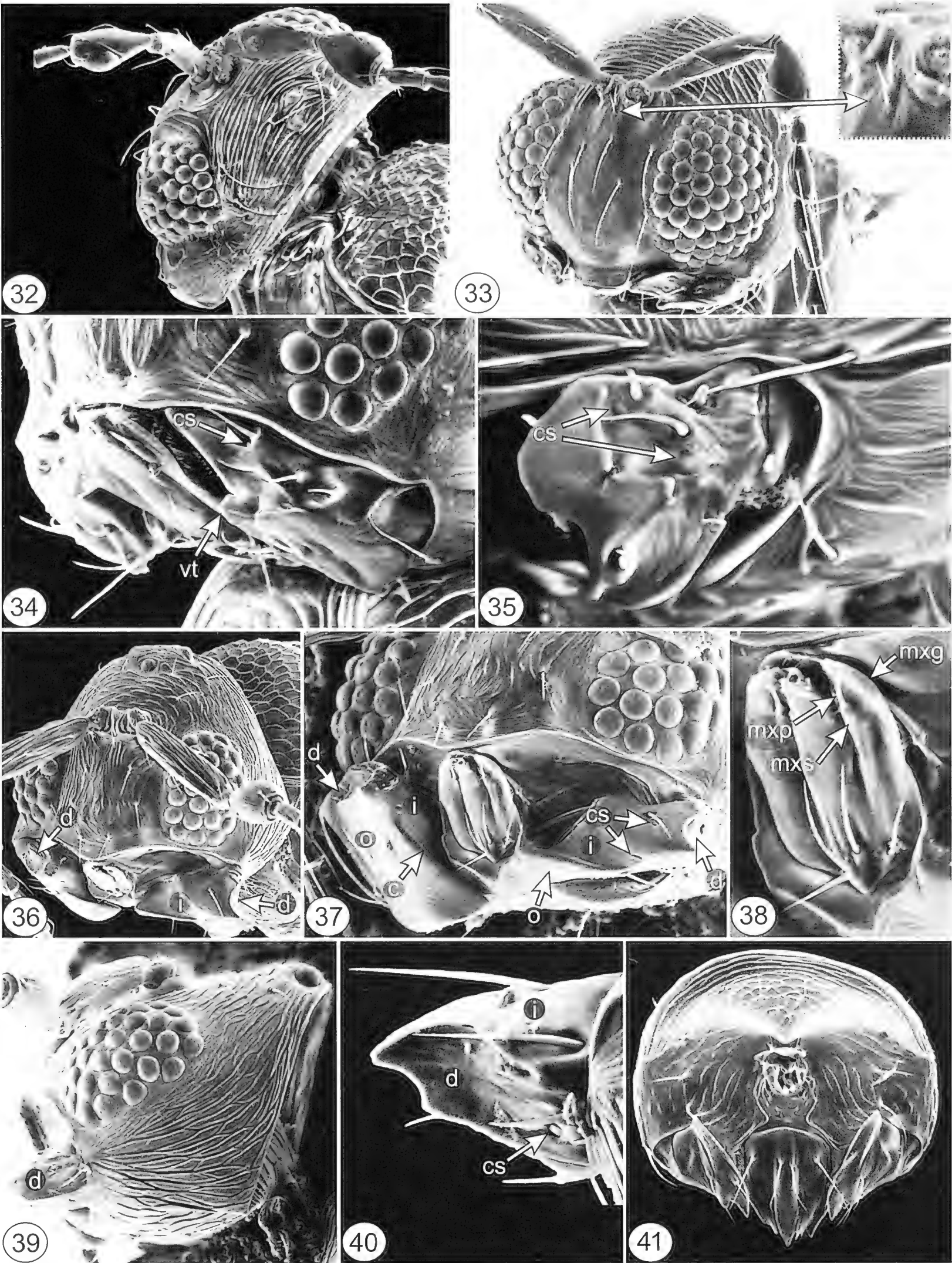


Figs 13-22. 13-15, head capsule: 13, *Mymaromella mira* (ocp expanded); 14, *Mymaromma anomalum* (ocp normal); 15, *Mymaromma buyckxi* (ocp inflexed). 16 and 17, *M. anomalum*, articulation of occipital and frontal plates: 16, posterolateral; 17, lateral. 18, *M. buyckxi*, mouthparts and propleura. 19, *M. anomalum*, head, anteroventral (insert: posterior tentorial pits). 20-22, *Mymaromma* spp., labiomaxillary complex: 20, *M. anomalum*, ventral; 21, *M. sp. 7*, anteroventral; 22, *M. sp. 6*, anterolateral.



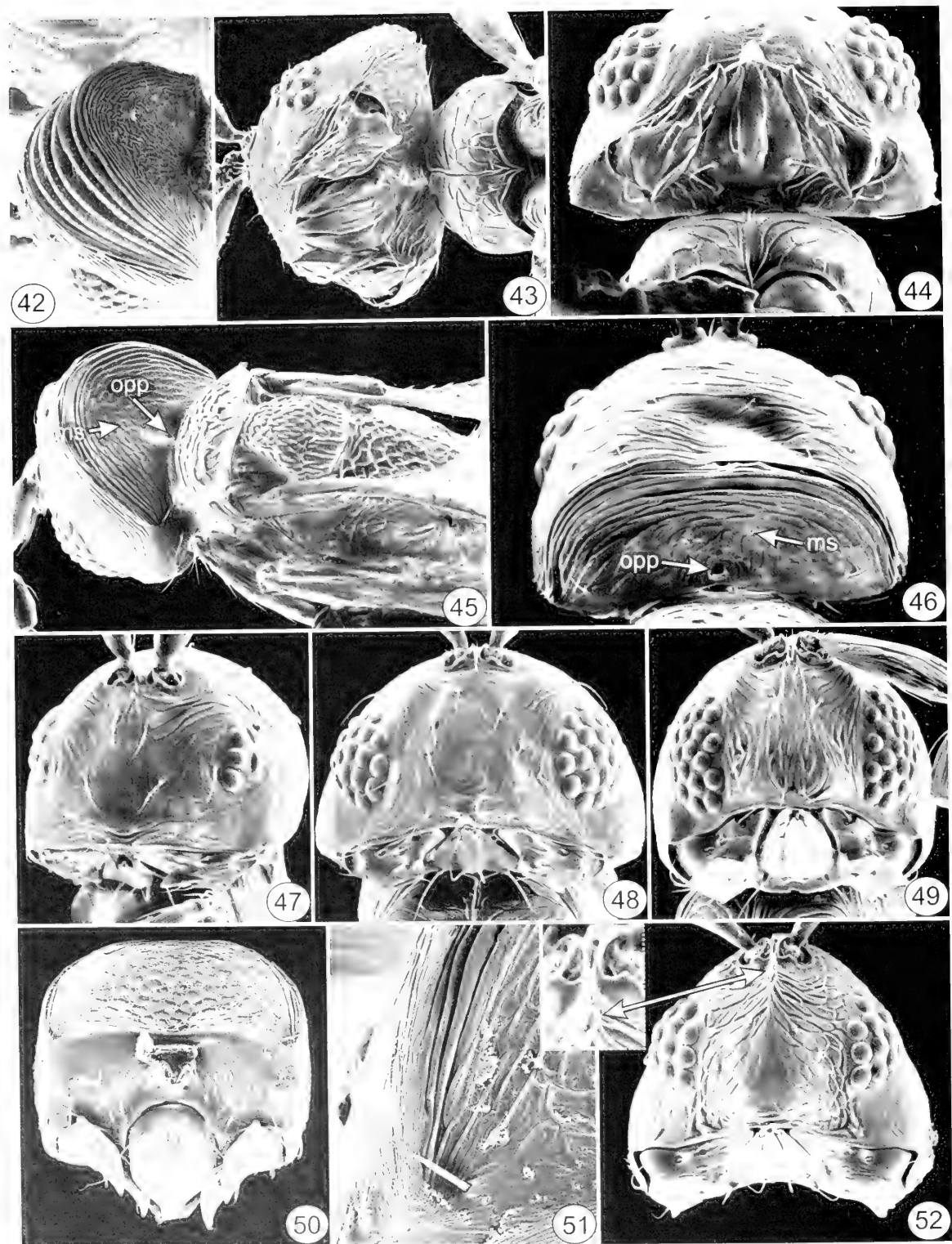


Figs 23–31. *Mymaromma* spp. 23, *M. sp. 6*, head, posterior. 24, *M. sp. 7*, occipital foramen. 25, *M. sp. 6*, head, frontolateral. 26, *M. sp. 6*, mandible (insert: apex of mandible). 27, *M. anomalum*, mandible. 28, *M. sp. 10*, head, frontal. 29, *M. goethei*, head, lateral. 30, *M. sp. 10*, head lateral. 31, *M. sp. 9*, head, frontal (insert: labiomaxillary complex).

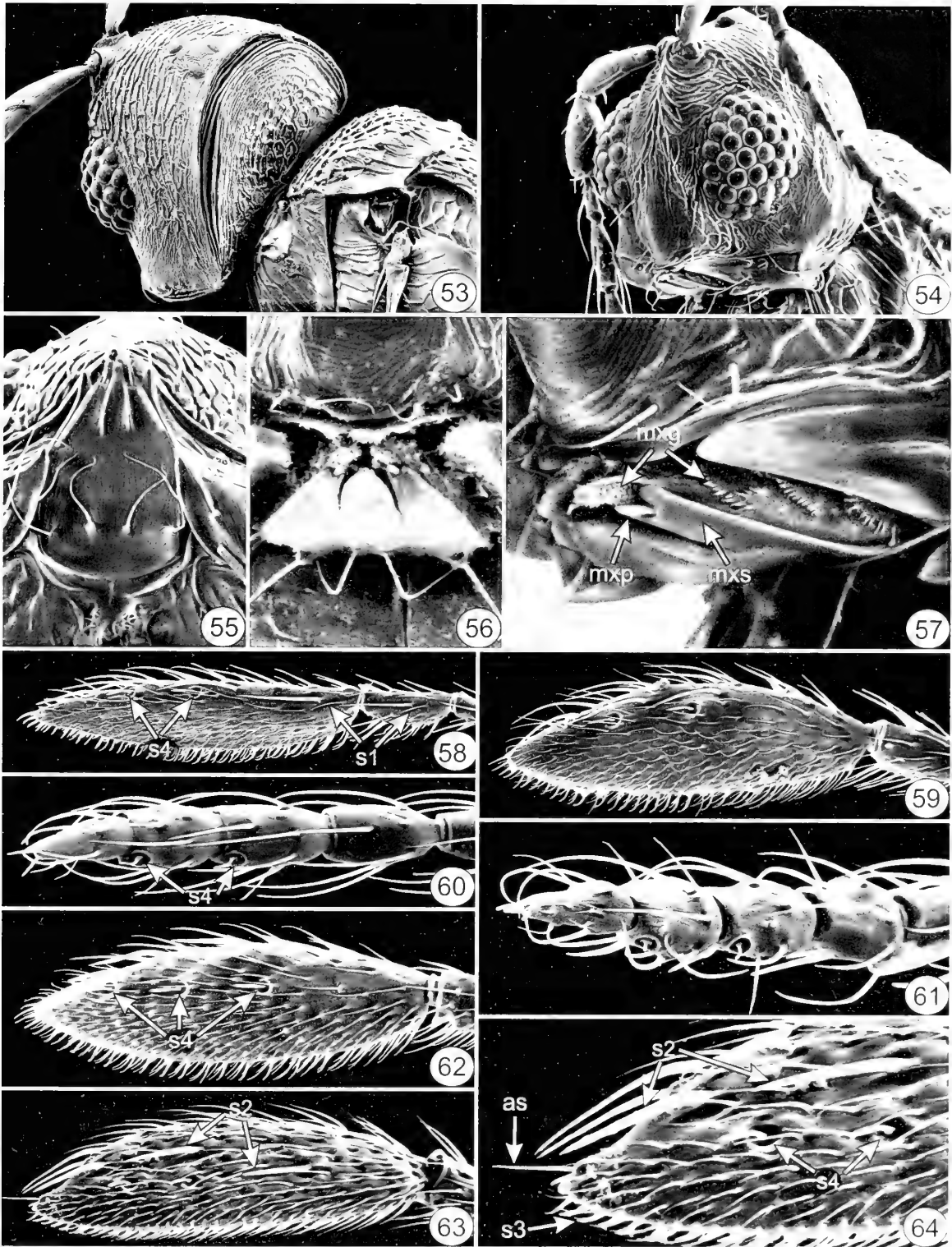


Figs 32–41. 32 and 33, *Mymaromma* spp., head: 32, *M.* sp. 9, dorsal; 33, *M. buyckxi*, frontolateral (insert: subtorular setae). 34, *Mymaromella* sp. 17, mouthparts, frontolateral. 35, *Mymaromella mira*, apex of mandible. 36–40, *Mymaromella* sp. 23: 36, head, frontolateral; 37, mouthparts; 38, labiomaxillary complex; 39, head, lateral; 40, mandible, outer view. 41, *Mymaromella* sp. 14, head, posterior.



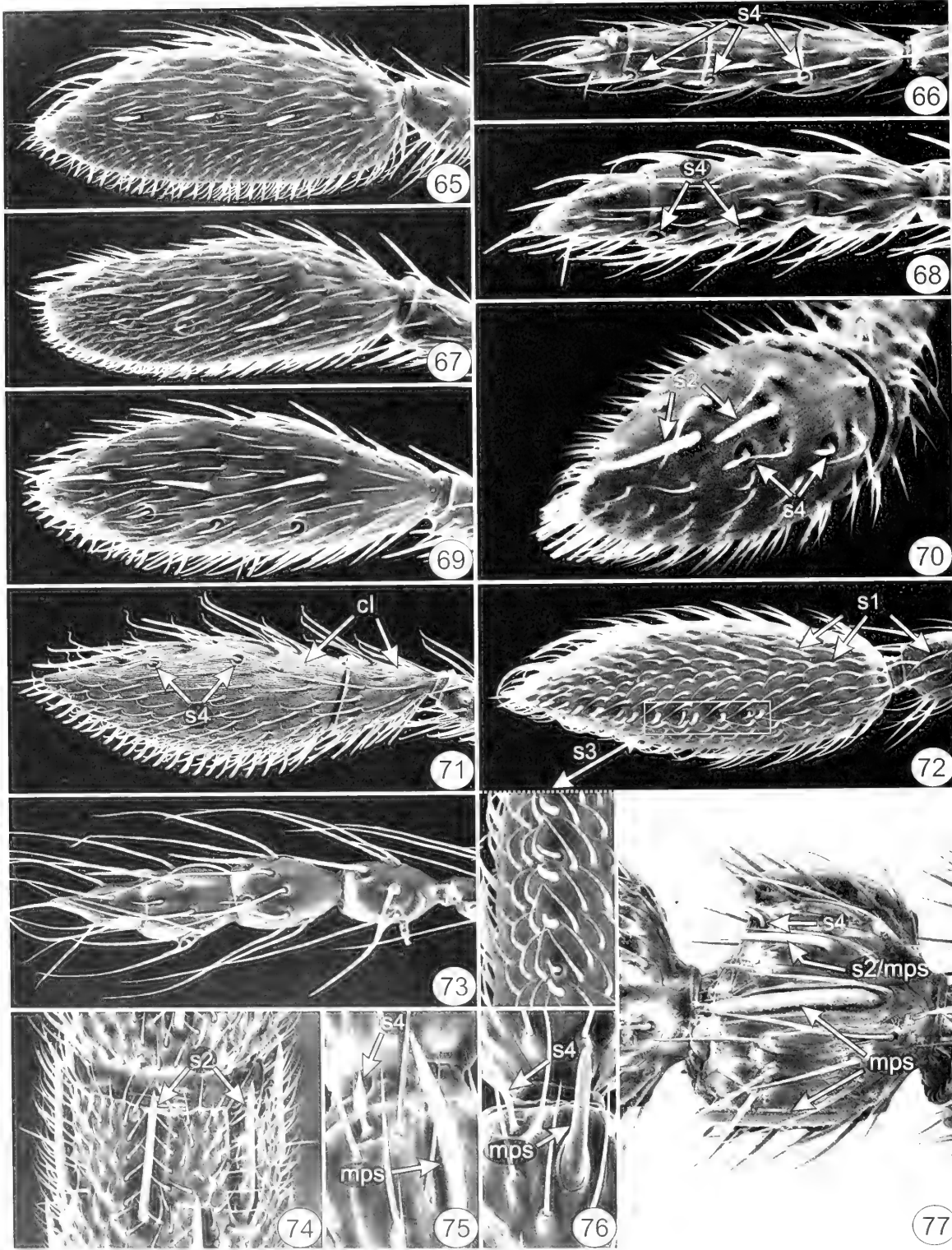


Figs 42–52. 42, *Mymaromma* sp. 8, occipital plate and pleated membrane. 43 and 44, *Mymaromella* spp., mouthparts and propleura: 43, *M.* sp. 15; 44, *M.* sp. 14. 45, *Mymaromella* sp. 17, head and mesosoma, dorsolateral. 46, *Mymaromella* sp. 16, head, dorsal. 47–49, *Mymaromella* spp., face and mouthparts: 47, *M.* sp. 20; 48, *M.* sp. 14; 49, *M.* sp. 17. 50 and 51, *Zealaromma valentini*: 50, head capsule, posterior; 51, articulation of occipital and frontal plates, posterior. 52, *Zealaromma insulare*, face and mouthparts (insert: subtorular setae).

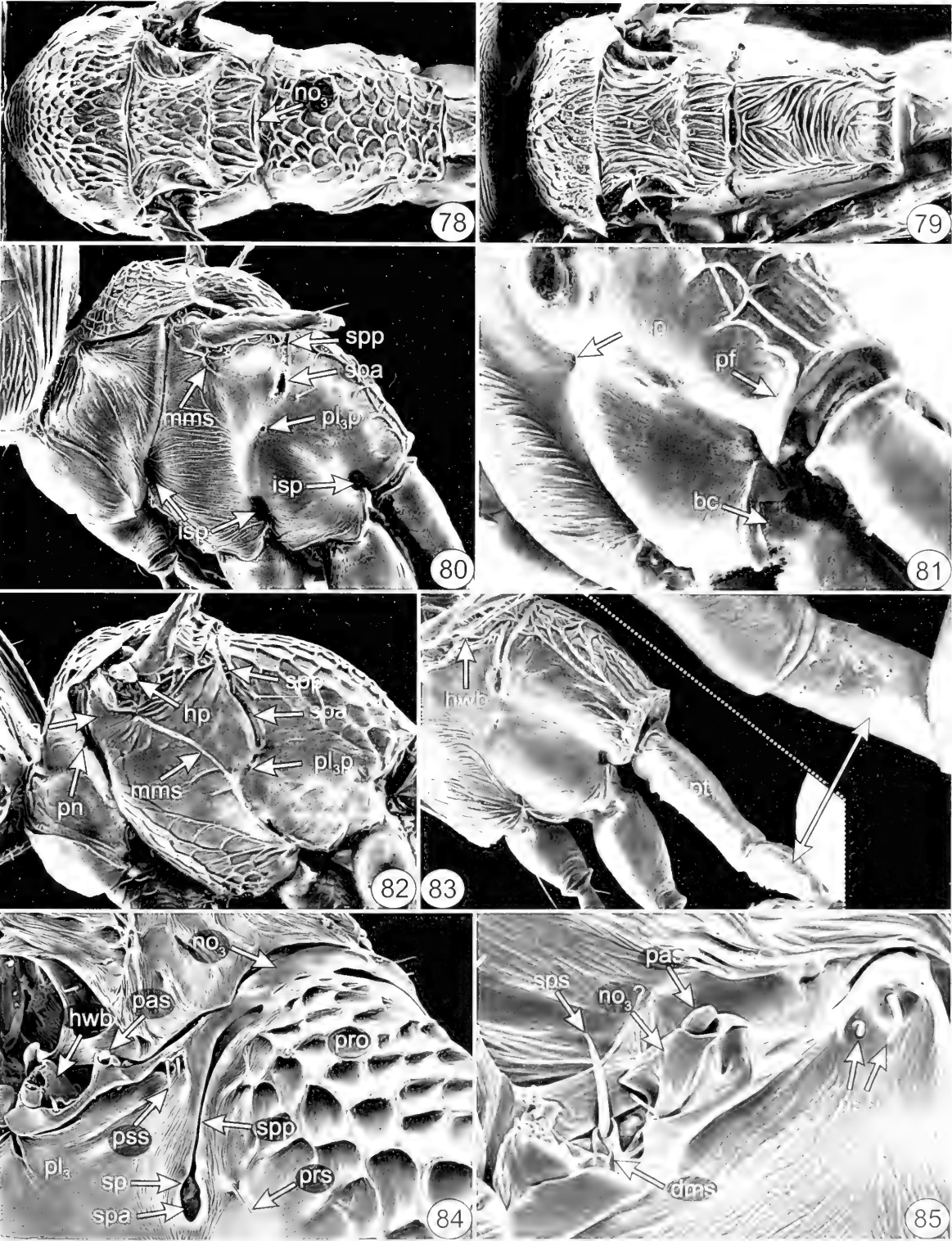


Figs 53–64. 53 and 54, *Zealaromma valentini*, head: 53, posterodorsal; 54, frontolateral. 55–57, *Zealaromma* spp., labiomaxillary complex: 55, *Z. insulare*, ventral; 56, *Z. valentini*, anterior; 57, *Z. valentini*, lateral. 58–61, *Mymaromma* spp., clava: 58, *M. sp.* 9 ♀; 59, *M. sp.* 10 ♀; 60, *M. goethei* ♂; 61, *M. anomalum* ♂. 62–64, *Mymaromella* spp., clava, outer surface: 62, *M. sp.* 21 ♀; 63, *M. sp.* 17 ♀; 64, *M. sp.* 17 ♀ (apical half).

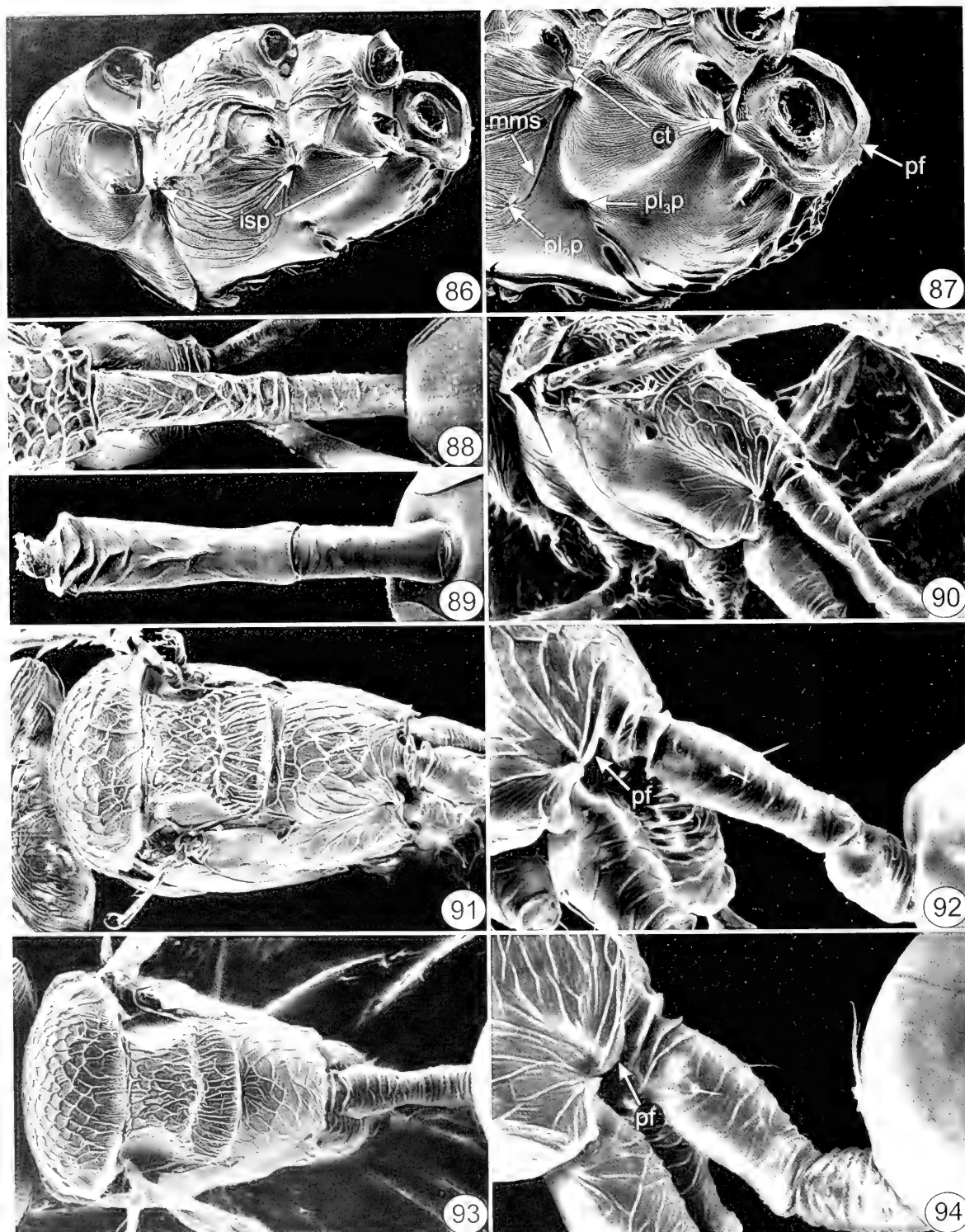




Figs. 65-77. 65-69, *Mymaromella* spp., clava: 65, *M. mira* ♀, outer; 66, *M. mira* ♂; 67, *M. sp.* 18 ♀, outer; 68, *M. sp.* 18 ♂; 69, *M. sp.* 23 ♀, outer. 70 and 71, *Zealaromma valentini* ♀, clava: 70, oblique dorsal; 71, outer. 72, *Mymaromella* sp. 20 ♀, clava, inner ventral (insert: different structures of s3-type sensilla). 73, *Z. insulare* ♂, clava. 74-77, ♀ tunicular segment: 74, *Maamunga rangi*; 75, *Chiloe micropteron*; 76, *Rotoita basalis*; 77, *Rotoita* sp. nr *R. basalis*.



Figs 78–85. 78 and 79, *Myrmaromma* spp., mesosoma, dorsal: 78, *M. buickyi*; 79, *M.* sp. 6. 80 and 81, *Myrmaromma* sp. 10: 80, mesosoma, lateral; 81, articulation of mesosoma and petiole, posterolateral. 82 and 83, *Myrmaromma* spp.: 82, *M.* sp. 9, mesosoma, lateral; 83, *M. goethci*, posterior of mesosoma and petiole, lateral (insert: second petiolar segment). 84 and 85, *Myrmaromma* sp. 7, metathoracic-propodeal complex: 84, posterolateral; 85, sensilla.

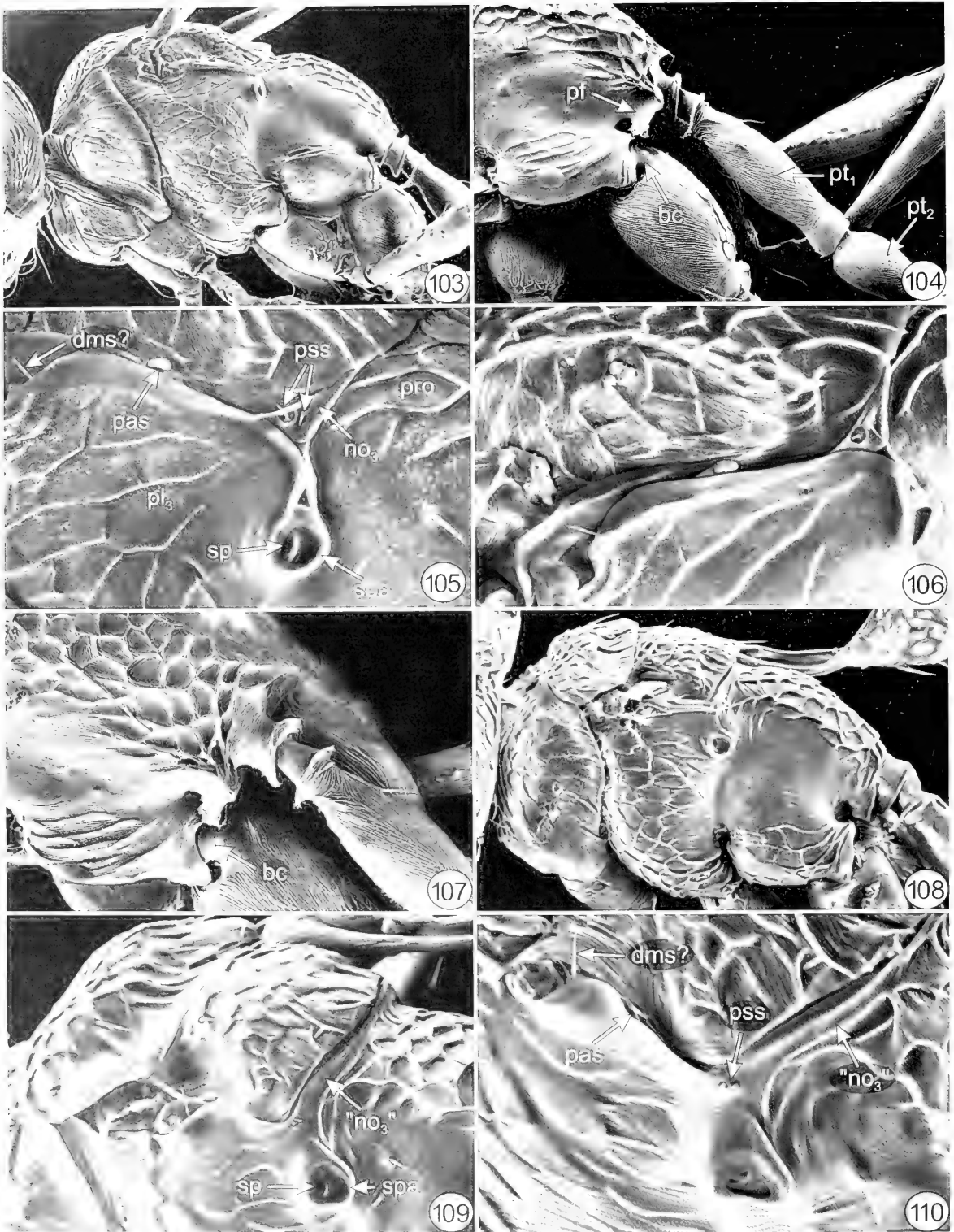


Figs 86-94. 86 and 87, *Myrmaromma* sp. 7: 86, mesosoma, ventrolateral; 87, posterior half of mesosoma, ventrolateral. 88 and 89, *Myrmaromma* spp., petiole: 88, *M. buyckvi*, dorsal; 89, *M.* sp. 6, ventral. 90, *Myrmaromella* sp. 21, mesosoma and petiole, posterolateral. 91 and 92, *Myrmaromella* sp. 14: 91, mesosoma, dorsal; 92, propodeal apex and petiole, lateral. 93 and 94, *Myrmaromella mira*: 93, mesosoma and petiole, dorsal; 94, propodeal apex and petiole, lateral.

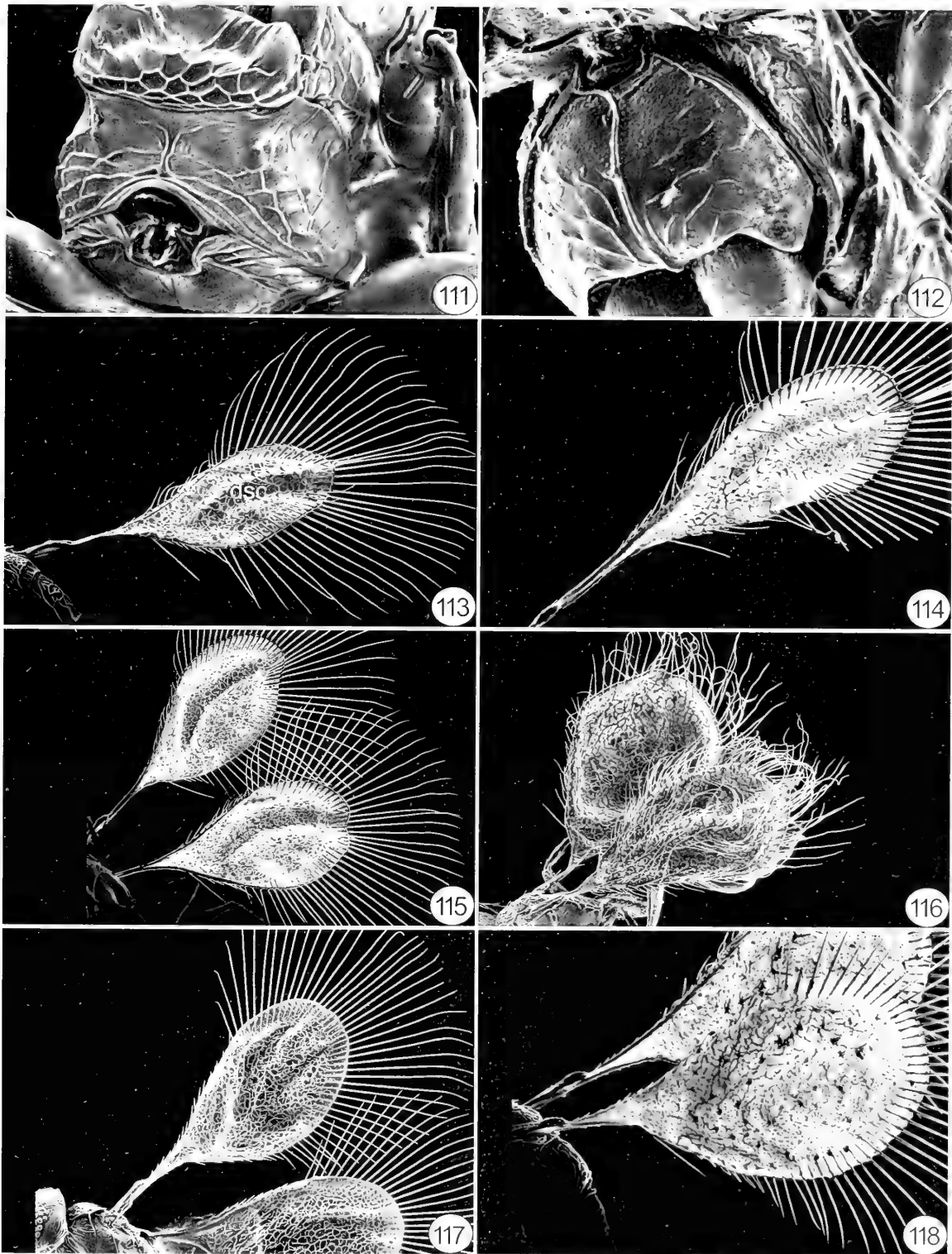




Figs 95–102. 95 and 96, *Mymaromella* spp., mesosoma, lateral: 95, *M.* sp. 21; 96, *M.* sp. 15. 97 and 98, *Mymaromella mira*: 97, mesosoma, lateral; 98, metathoracic-propodeal sensilla. 99 and 100, *Mymaromella* sp. 23: 99, mesosoma, lateral; 100, metathoracic-propodeal sensilla. 101 and 102, *Mymaromella* sp. 17: 101, mesosoma, lateral (insert: metapleural pit); 102, metathoracic-propodeal sensilla.

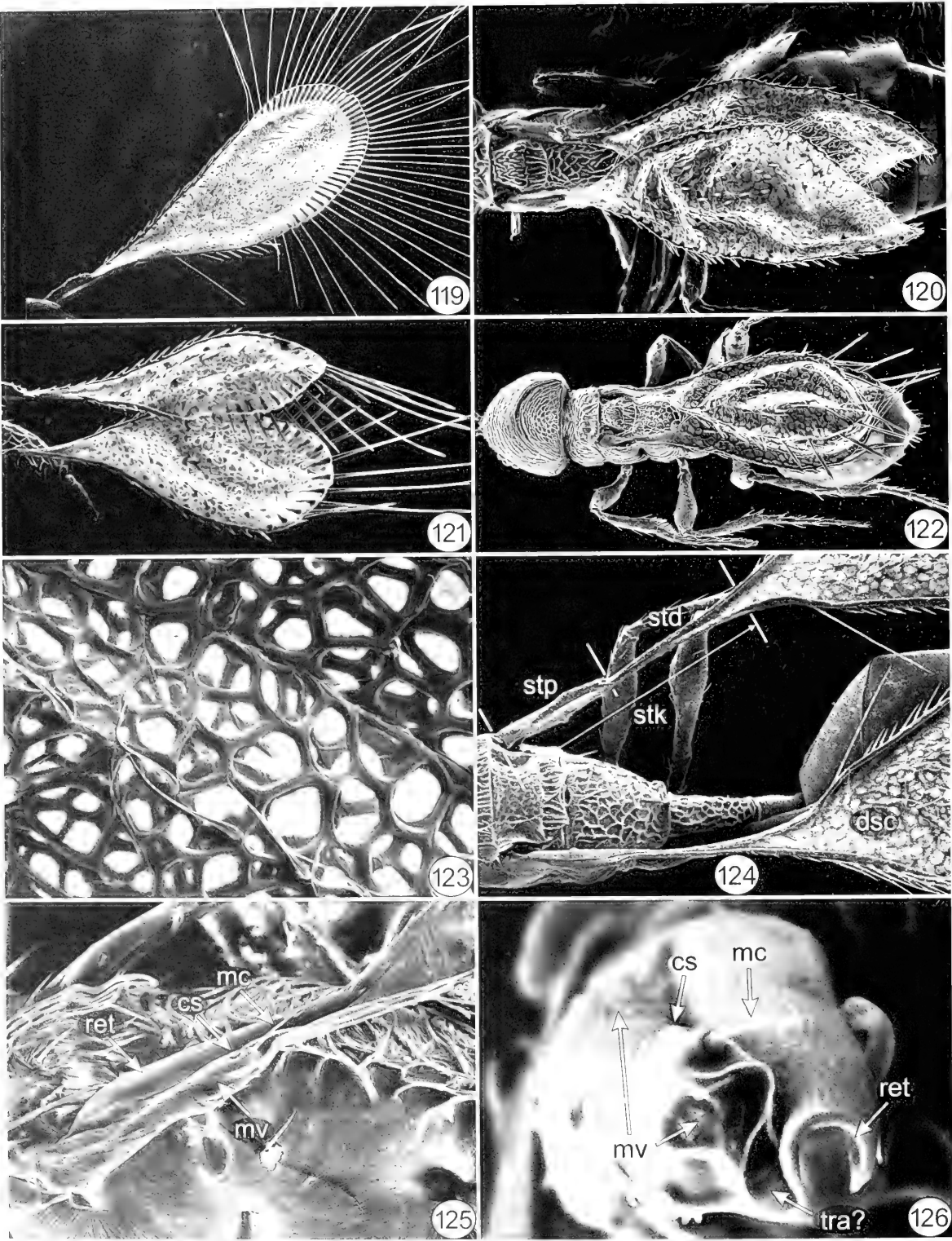


Figs. 103-110. 103-107, *Zecalaromma valentinii*: 103, mesosoma, lateral; 104, posterior of metasoma, lateral; 105, metathoracic-propodeal complex, lateral; 106, metathoracic-propodeal complex, dorsolateral; 107, posterior of metasoma, dorsolateral. 108-110, *Zecalaromma insulare*: 108, mesosoma, lateral; 109, metathoracic-propodeal complex, posterolateral; 110, metathoracic-propodeal complex, posterodorsal.



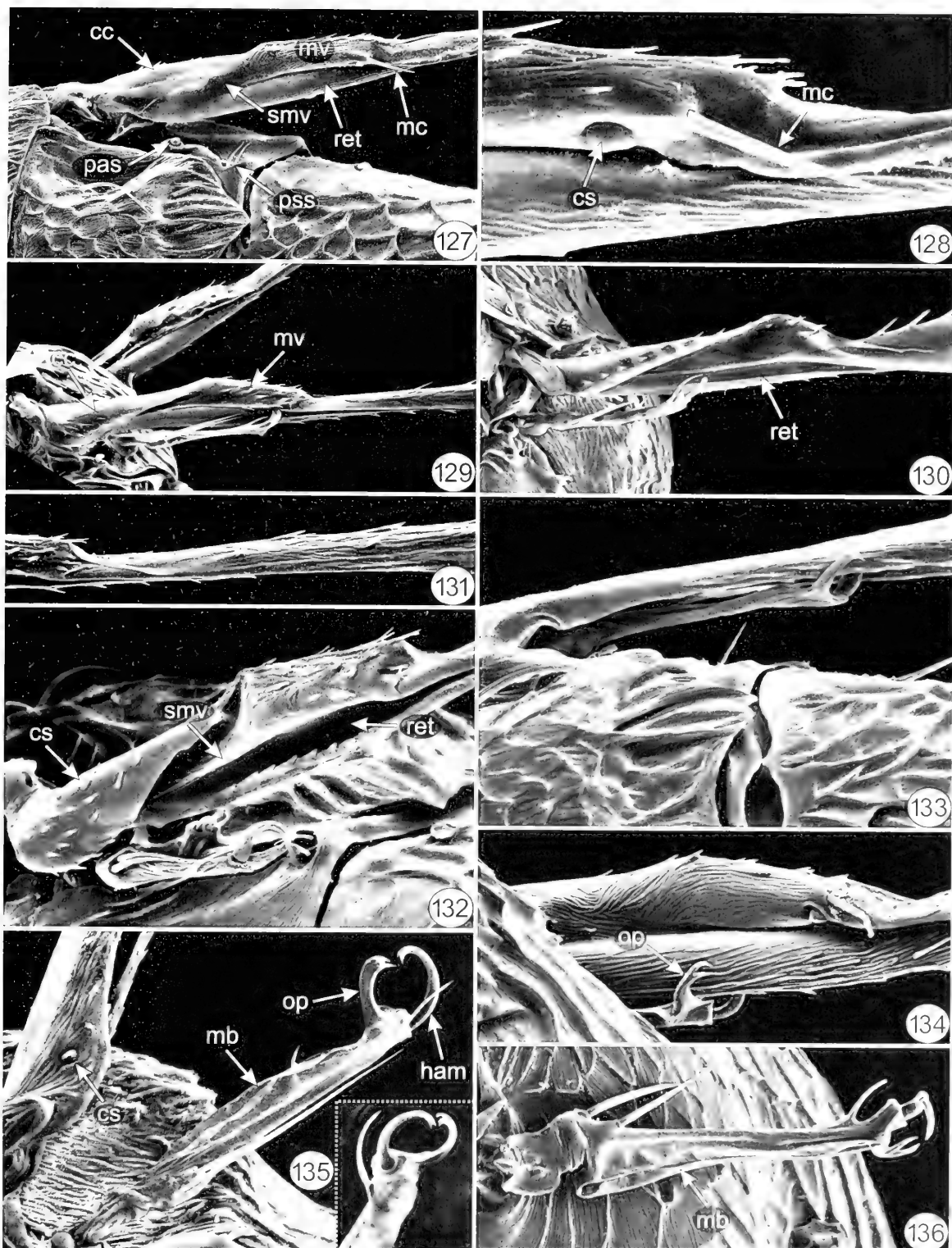
Figs 111–118. 111, *Zealaremma insulare*, mesosoma, anterior (head removed). 112, *Zealaremma calentini*, propleura, anteroventral. 113–116, *Mymaromma* spp., forewing: 113, *M. goetheri*; 114, *M. sp. 9*; 115, *M. buicki*; 116, *M. sp. 10*. 117 and 118, *Mymaromella* spp., forewing: 117, *M. sp. 14*; 118, *M. sp. 21*.



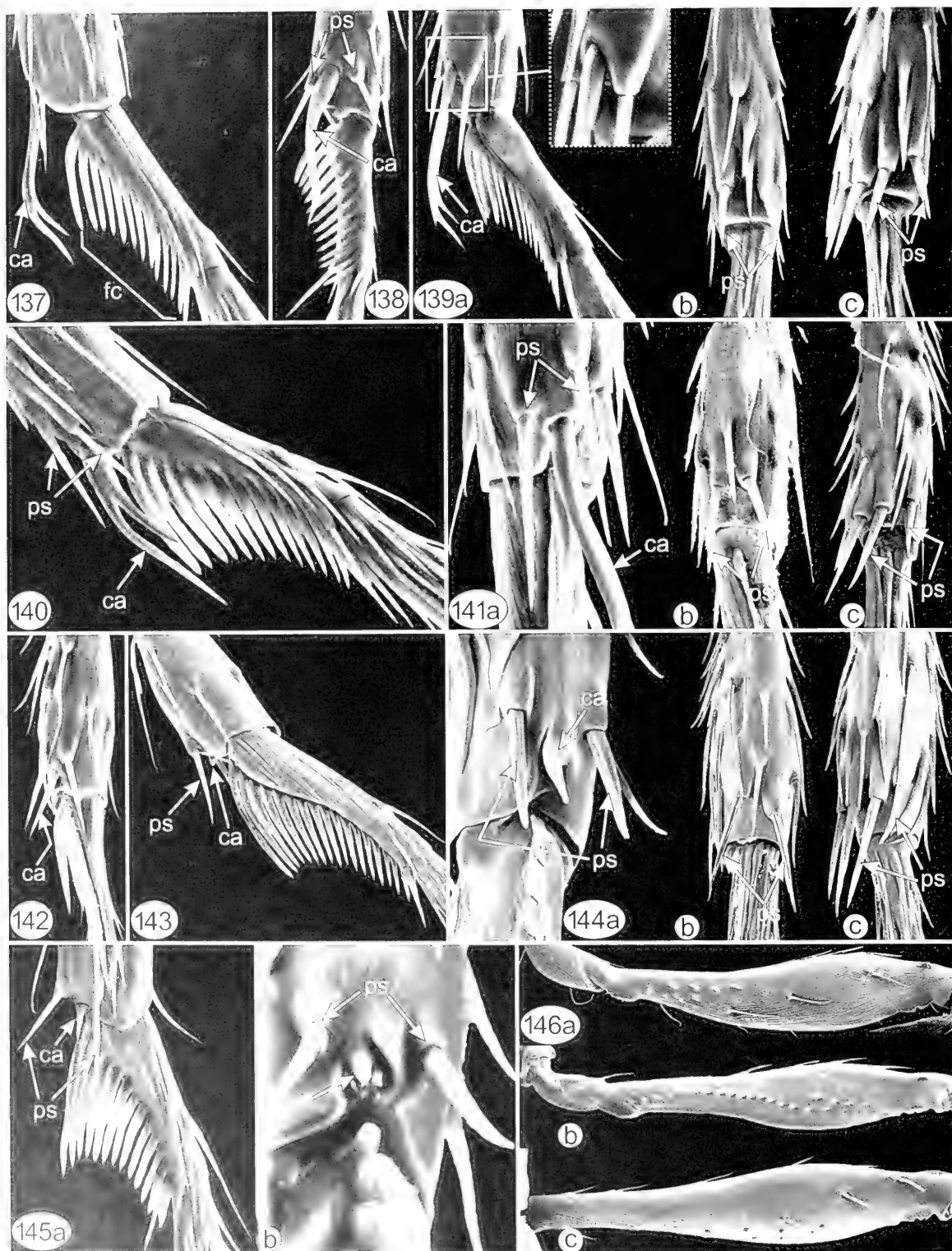


Figs 119–126. 119–121, *Mymaromella* spp., forewing: 119, *M.* sp. 18; 120, *M.* sp. 17; 121, *M.* sp. 20. 122, *Zealaromma insulare*, dorsal habitus. 123, *Zealaromma calentini*, forewing disc reticulate pattern. 124, *Mymaromma anomalum*, proximal part of forewing. 125 and 126, *Mymaromma* sp. 10: 125, proximal part of forewing; 126, cross-section of forewing venation

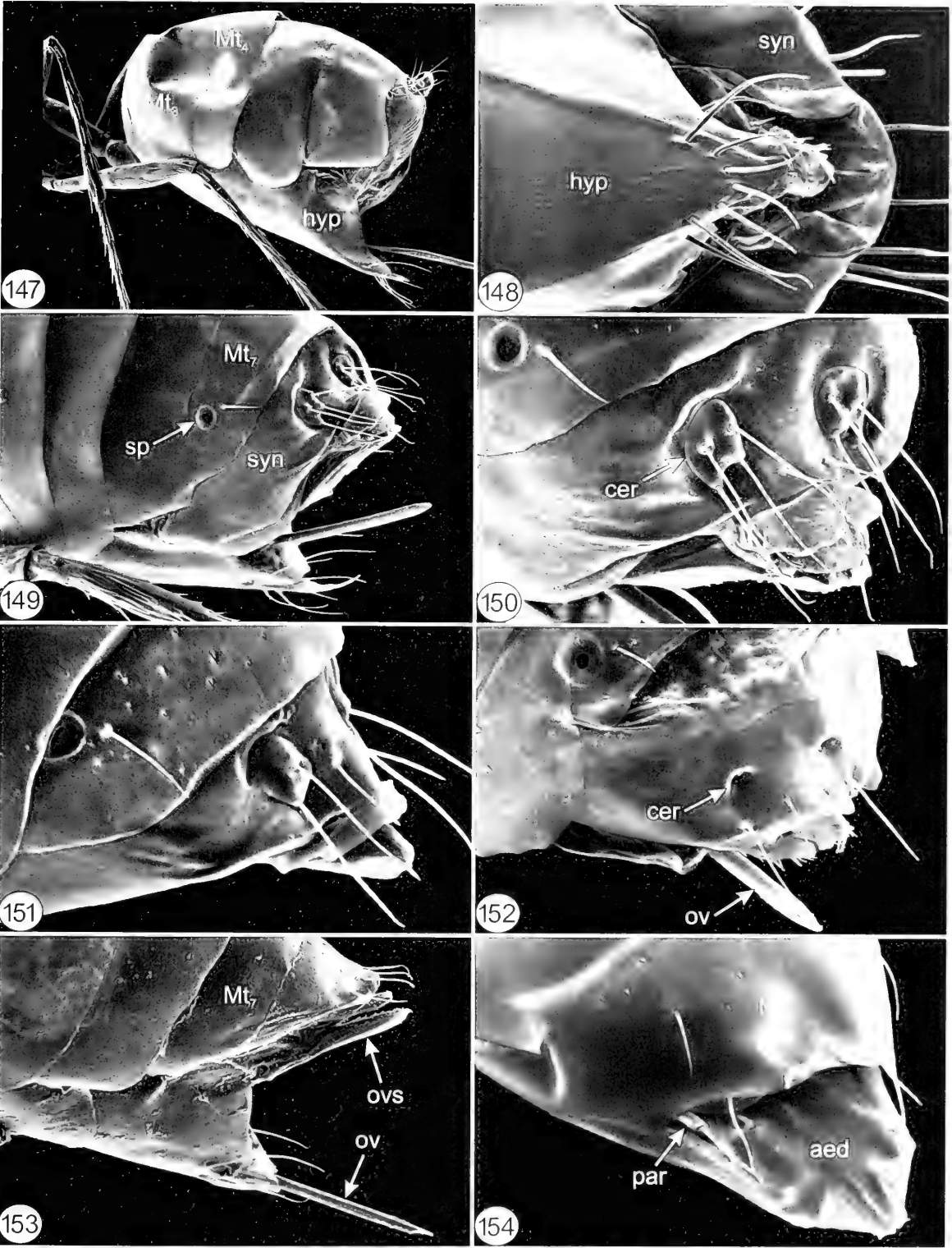




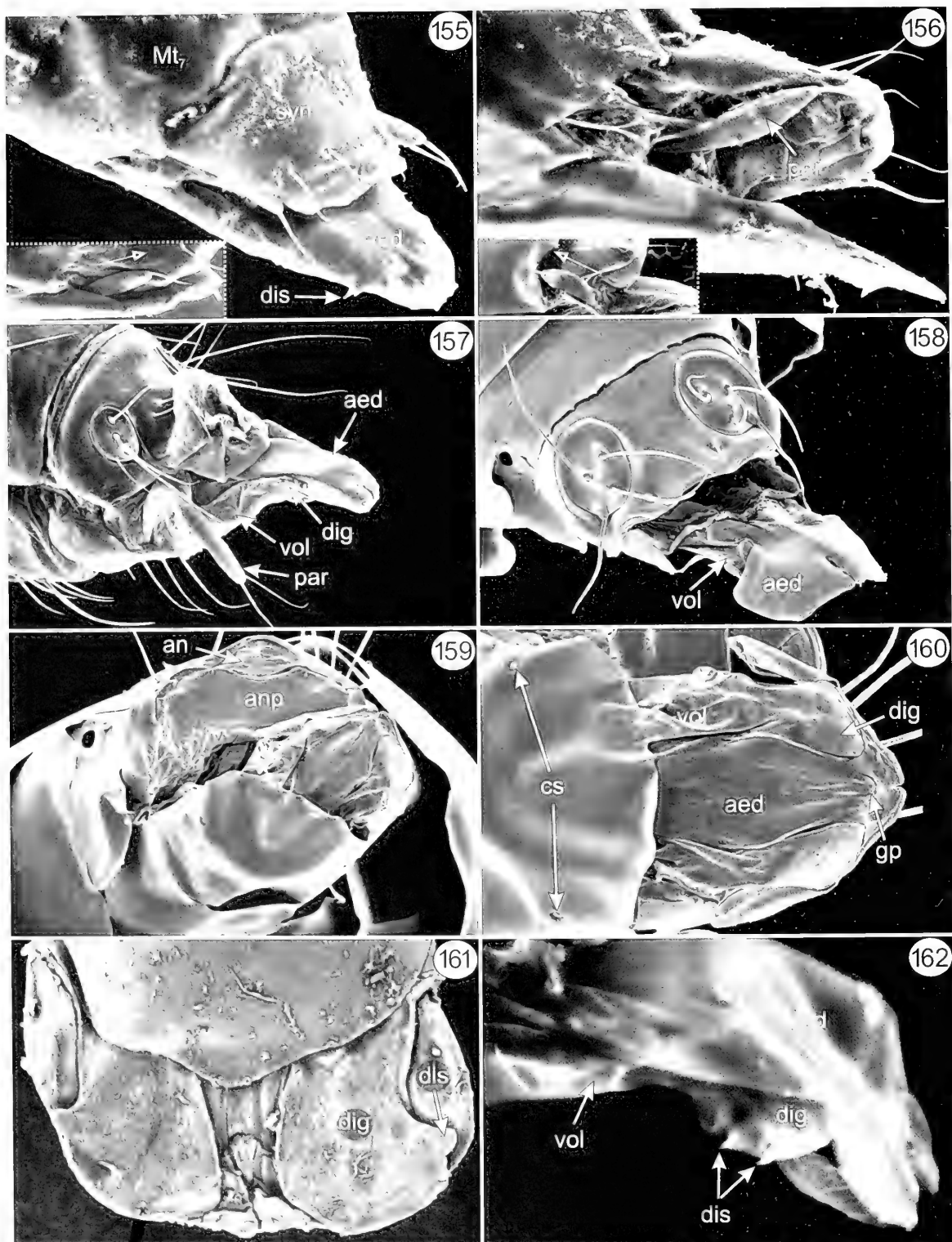
Figs 127–136. 127 and 128, *Mymaromella anomalum*: 127, proximal part of forewing stalk, dorsal; 128, apex of forewing venation. 129 and 130, *Mymaromella goethici*: 129, proximal part of forewing stalk, ventral; 130, *Mymaromella* sp. 14. 131–133, *M. anomalum*: 131, distal part of forewing stalk, ventral; 132, proximal part of forewing stalk, ventral; 133, wing coupling, dorsal. 134, *Zecalaromella calentimici*, wing coupling. 135 and 136, hind wing: 135, *Mymaromella* sp. 23 (insert: apex, *Mymaromella* sp. 18); 136, *Zecalaromella calentimici*.



Figs. 137–146. 137 and 138, strigil: 137, *Mymaromella* sp. 17, lateral; 138, *Mymaromella* sp. 21, ventrolateral. 139, *Mymaromella* sp. 14: a, strigil, lateral (insert: enlargement of calcar base between pseudospurs); b and c, apex of tibia, ventral: b, mesotibia; c, metatibia. 140 and 141, *Zecalaromma valentini*: 140, strigil, lateral; 141, apex of tibia, ventral: a, protibia; b, mesotibia; c, metatibia. 142, *Mymaromma goethci*, strigil, ventral. 143 and 144, *Mymaromma anomalum*: 143, strigil, lateral; 144: apex of tibia, ventral: a, protibia; b, mesotibia; c, metatibia. 145, *Mymaromma* sp. 10: a, strigil, lateral; b, apex of protibia, ventral (calcar foreshortened). 146, *Z. valentini*, femur, posterior surface: a, protemur; b, mesotemur; c, metatemur.

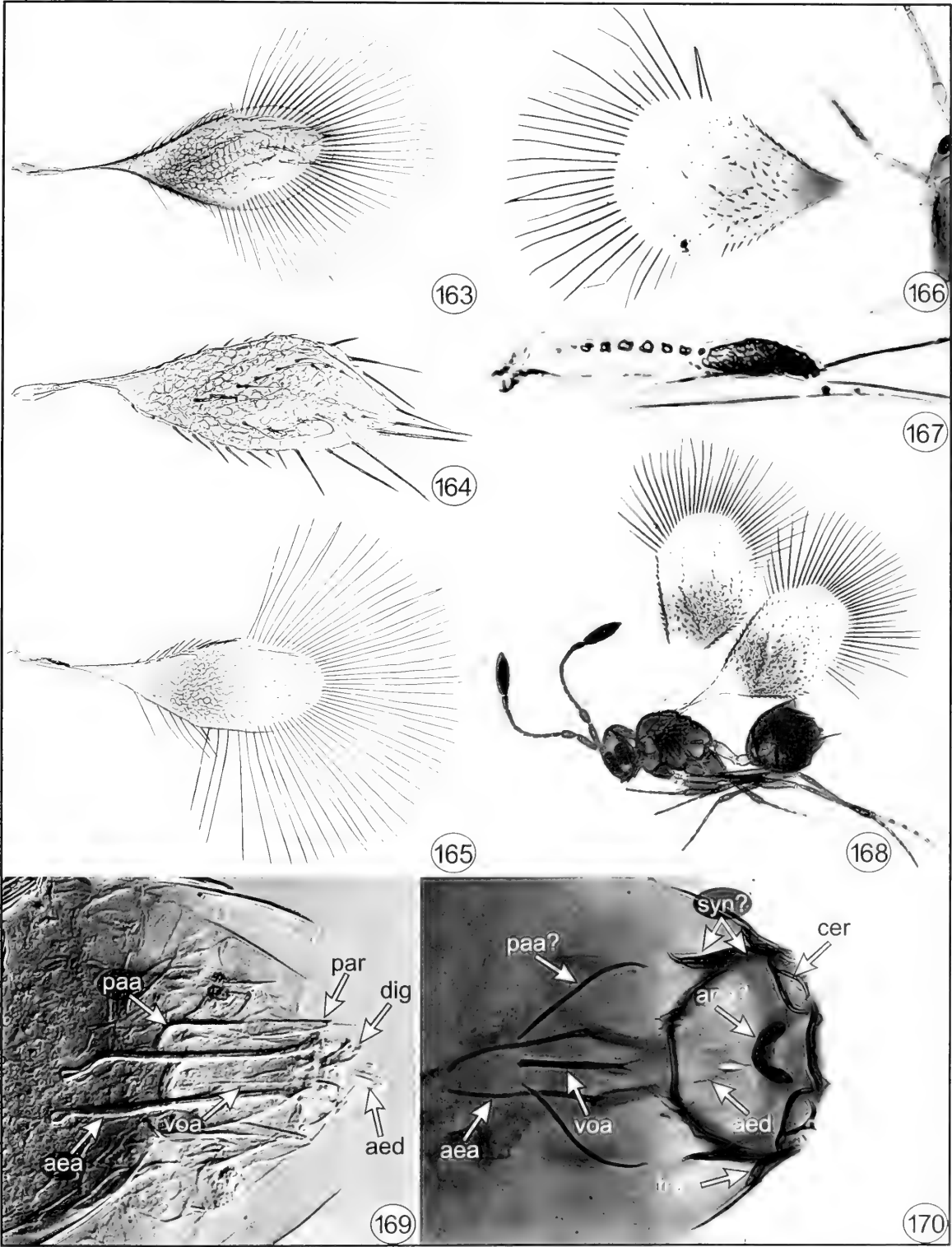


Figs 147–154. 147, *Mymaromella* sp. 23 ♀, gaster. 148, *Mymaromella* sp. 6 ♀, hypopygium. 149 and 150, *Mymaromella* sp. 18 ♀: 149, apex of gaster; 150, apical two gastral tergites. 151 and 152, ♀, apical two gastral tergites: 151, *Mymaromella* sp. 17; 152, *Mymaromella* sp. 10. 153 and 154, *Zcalaromma* spp.: 153, *Z. calantmex* ♀, apex of gaster; 154, *Z. insulare* ♀, penultimate gastral tergite and aedeagus (syntergum concealed under  $Mt_7$ ).

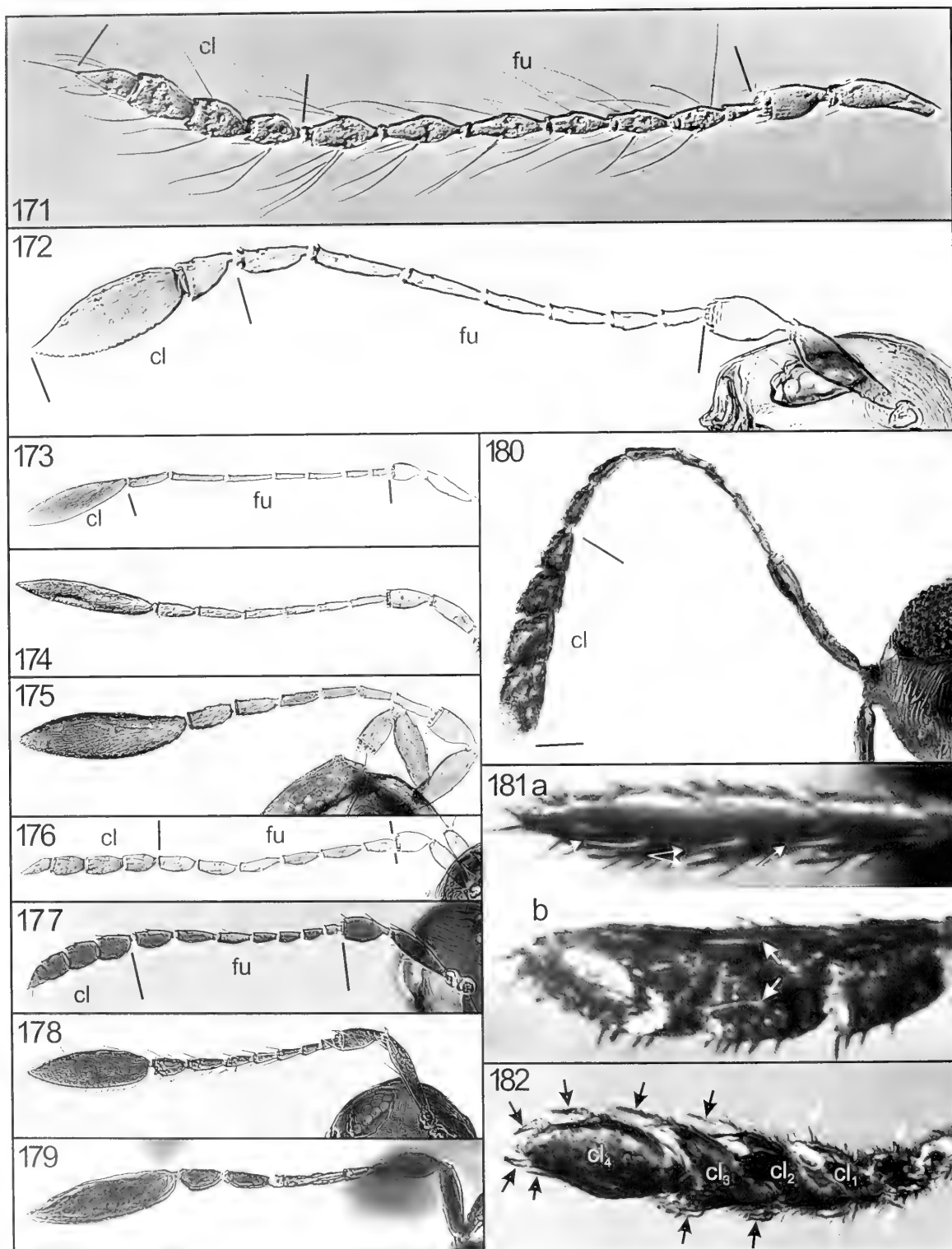


Figs 155–162. 155 and 156, *Zealaromma valentini* ♂, apex of gaster (insert: paramere, arrows indicate direction): 155, dorsolateral; 156, ventrolateral. 157, *Maaminga rangi* ♂, Mt<sub>8</sub> and genitalia. 158–160, *Mymaromma* sp. 7 ♂, apex of gaster and genitalia: 158, dorsolateral; 159, ventrolateral; 160, ventral. 161, *Mymaromma* sp. 6 ♂, parameres, ventral. 162, *Mymaromella mira* ♂, genitalia, dorsolateral.

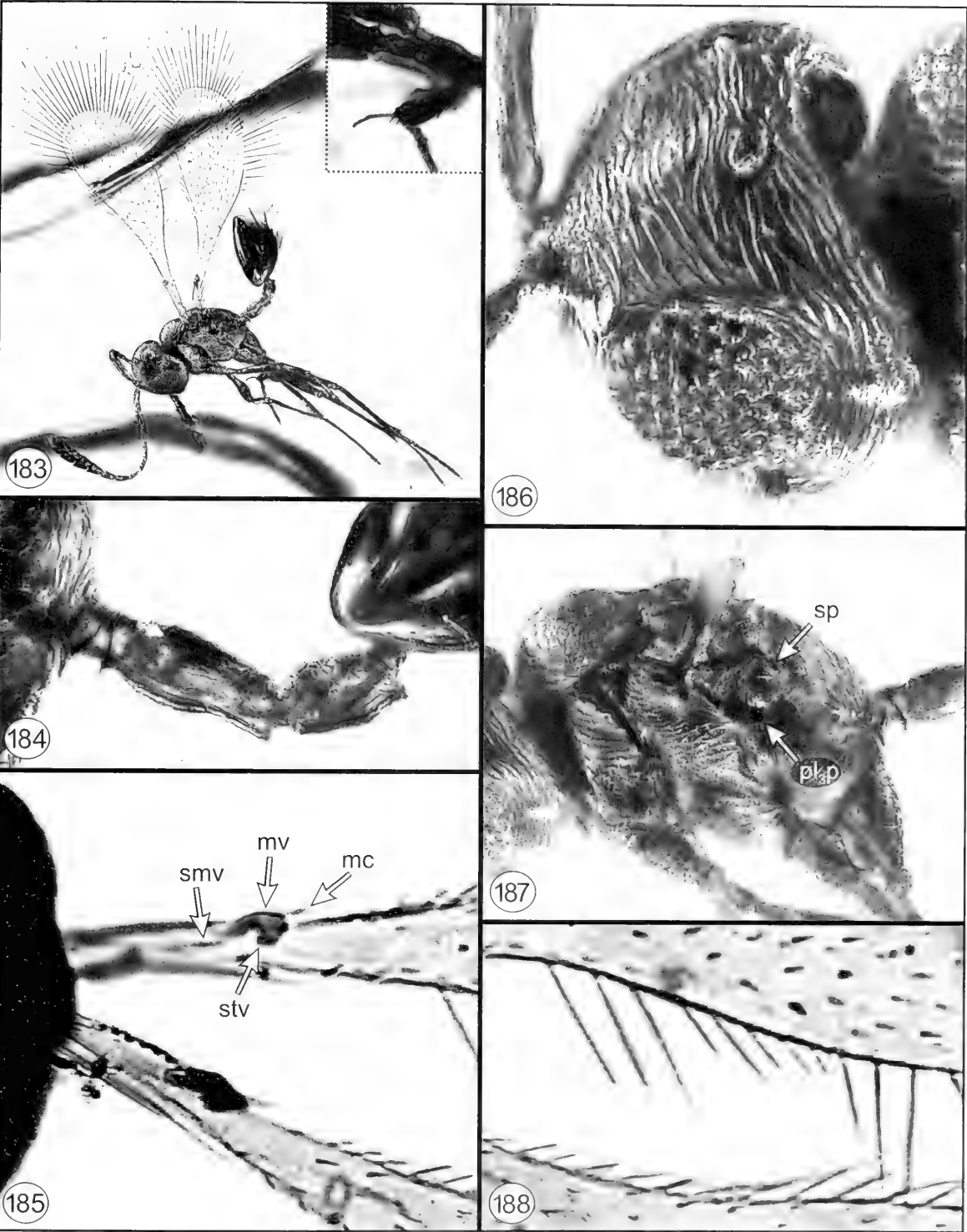




Figs 163–170. 163–166, forewing: 163, *Mymaromma anomalum* (Sweden); 164, *Zealaromma insulare*; 165, *Z. valentinei*; 166, *Mymaromella cyclopterus* (holotype ♀). 167, *Mymaromella* sp. 14, forewing stalk. 168, *Mymaromella mira* (USNM type photograph). 169 and 170, ♂ genitalia: 169, *Z. insulare*; 170, *M. anomalum* (Japan).

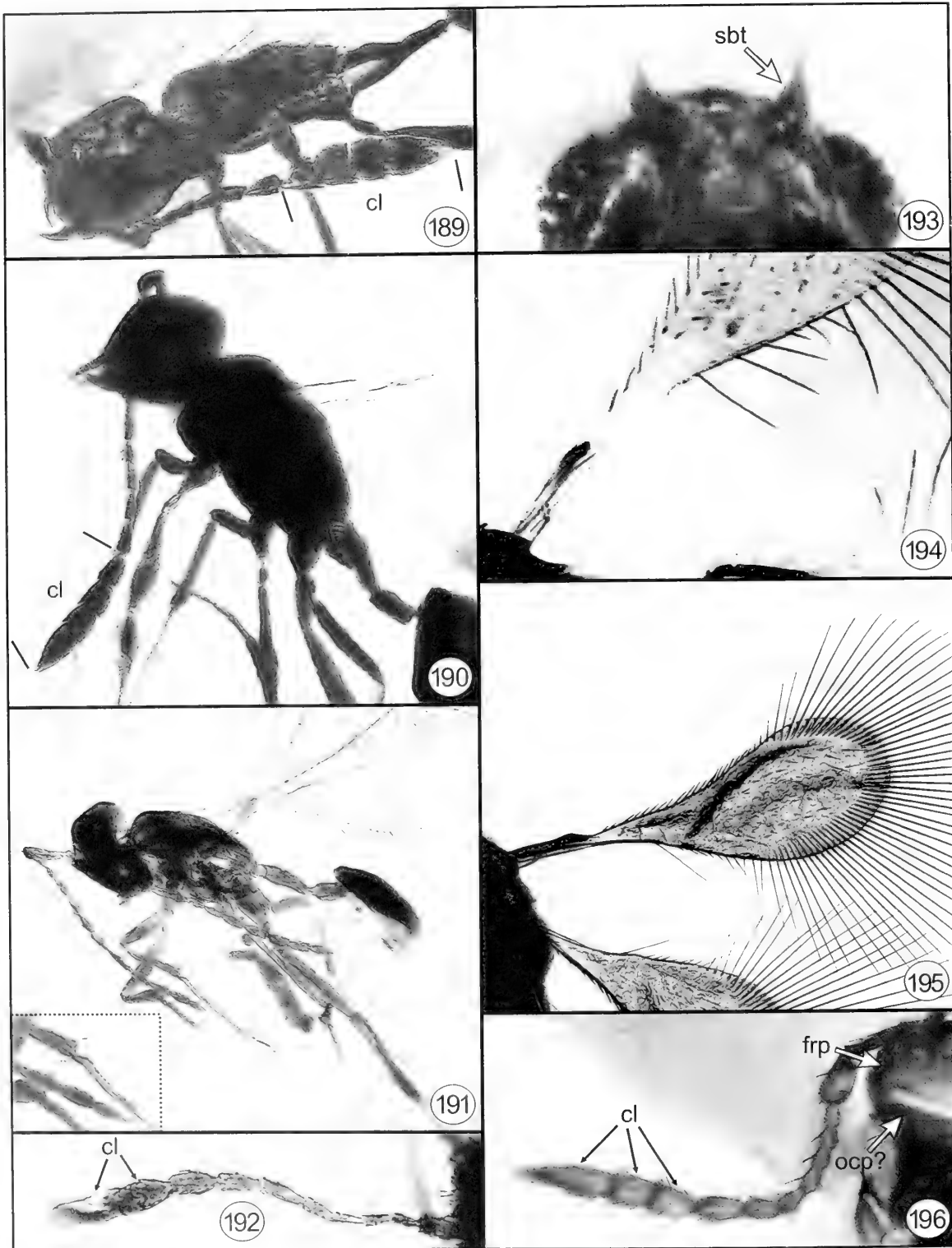


Figs 171–182. 171 and 172, *Zealaromma* spp., antenna: 171, *Z. insulare* ♂; 172, *Z. valentini* ♀. 173–176, *Mymaromma* spp., antenna: 173, *M. anomalum* ♀; 174, *M. goethei* ♀; 175, *M. sp. nr goethei* ♀; 176, *M. sp. nr goethei* ♂. 177 and 178, *Mymaromella* sp. 14, antenna: 177, ♀; 178, ♂. 179, *Palacomymar succini* ♀, antenna. 180 and 181, *Galloromma agapa* (holotype ♀): 180, left antenna; 181, apical three claval segments (a, right clava, dorsal view; b, left clava, outer surface). 182, *Galloromma* sp. ♀, clava (GPPC: HY17A). (Arrows point to sensilla in Figs 181, 182.)

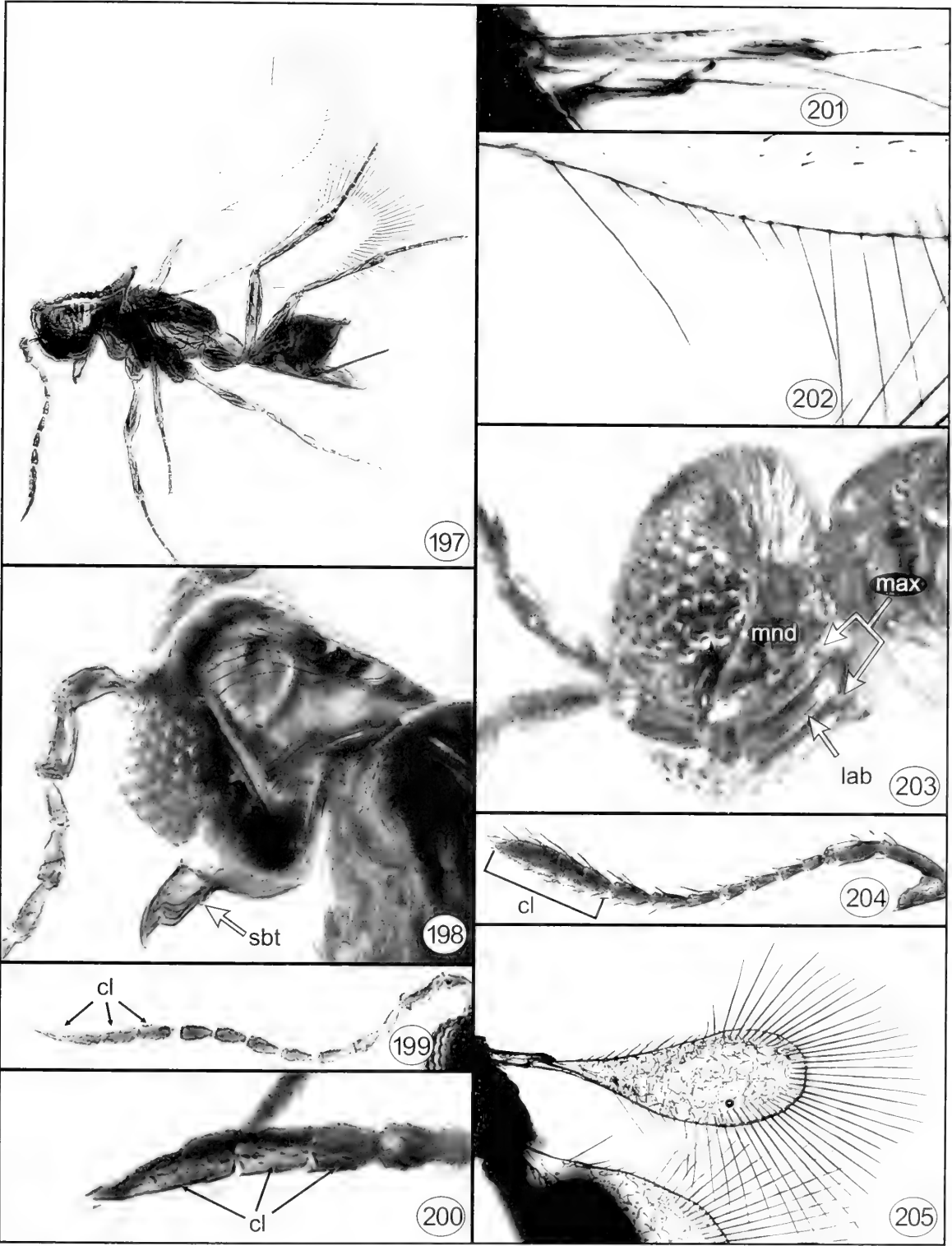


Figs 183–188. 183–188, *Galloromma agapa* (holotype ♀): 183, habitus (insert: calcar); 184, petiolar segments; 185, proximal part of forewings; 186, head, dorsolateral; 187, mesosoma, lateral; 188, forewing posterobasal marginal setae.

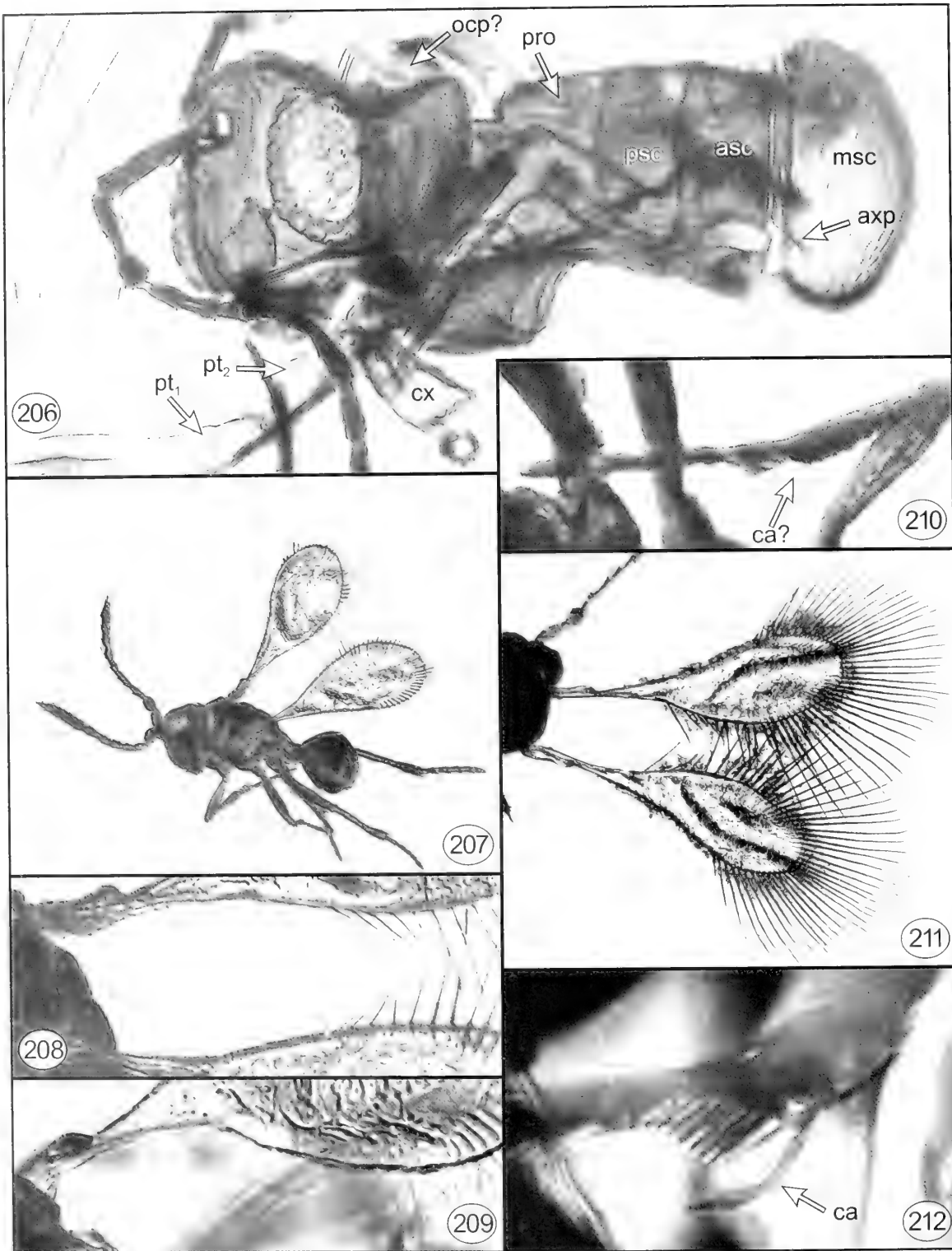




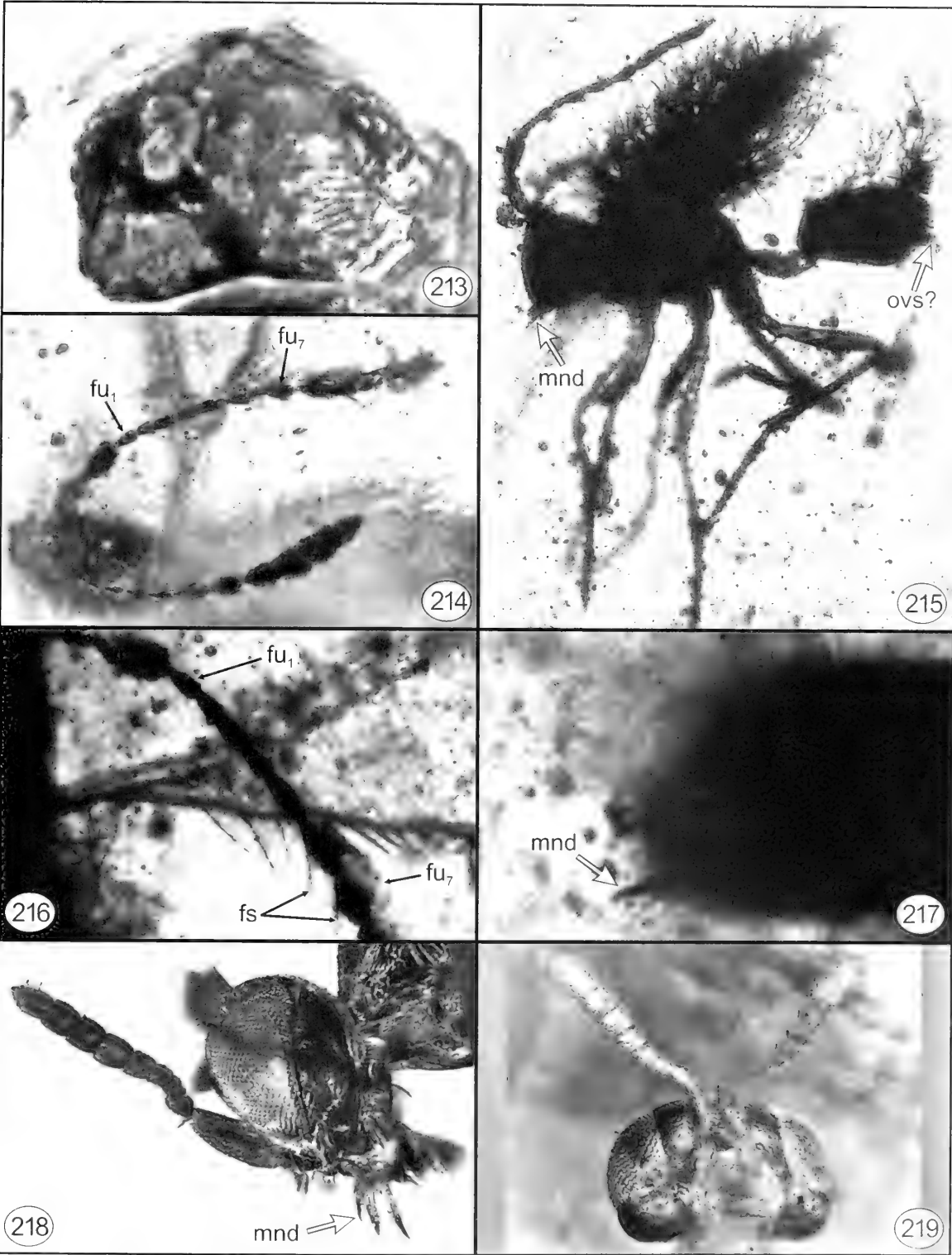
Figs 189–196. 189–191, *Galloromma* sp. (AMNH: B-0107): 189, ♀ head and antenna, dorsal; 190, ♀ body except gaster, lateral; 191, ♂ habitus (insert: calcar). 192, *Archaeromma minutissimum*, antenna (holotype ♀). 193, *Galloromma* sp. ♀, mandibles, ventral (GPPC: HY17A). 194, *Archaeromma nearcticum* ♀, forewing posterobasal marginal setae (CNC: CAS-598). 195, *Archaeromma* sp. ♂, forewing (AMNH: NJ-179). 196, *Archaeromma masneri*, head (dorsal) and antenna (holotype ♀).



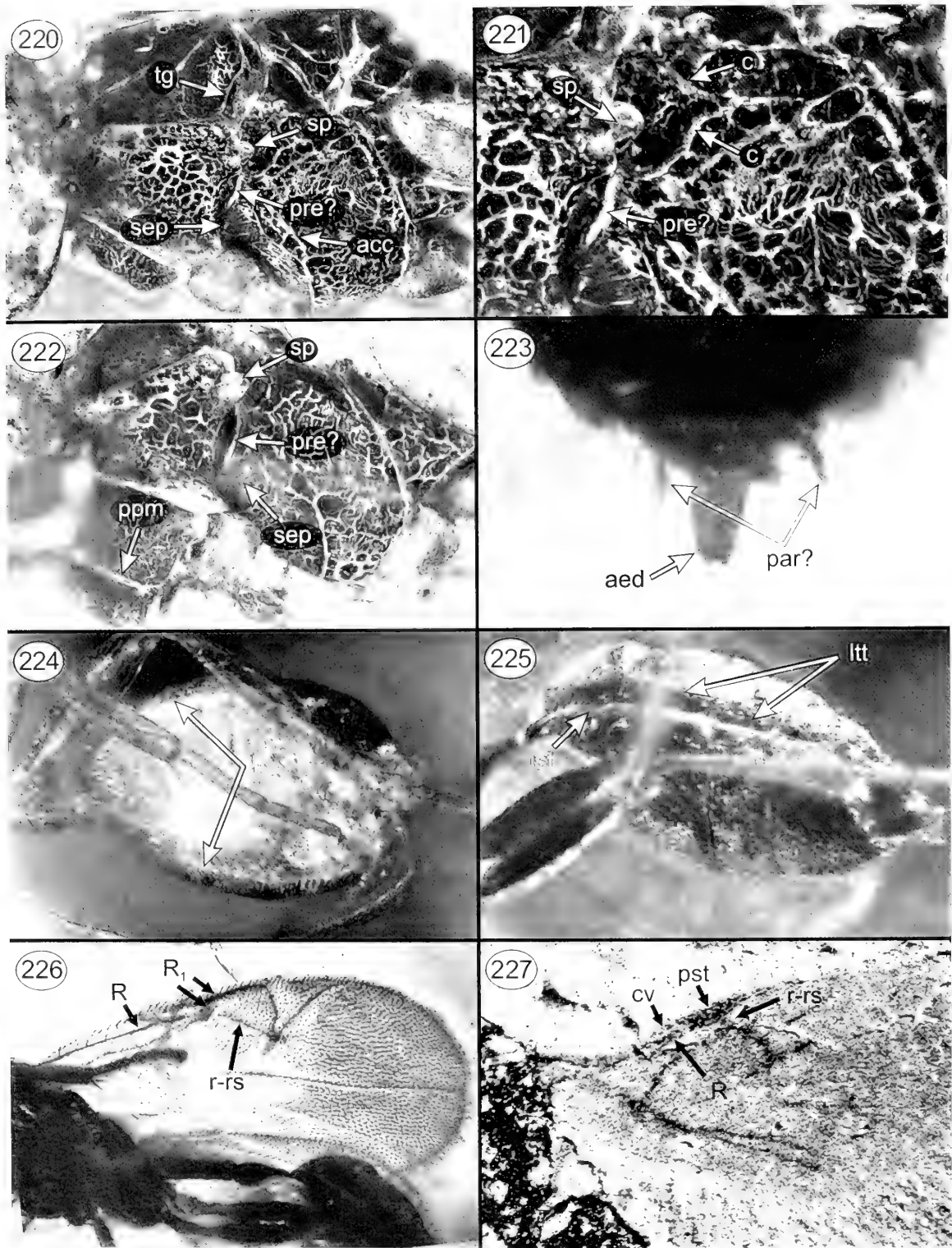
Figs 197–205. 197–202, *Archaeromma mandibulatum* (holotype ♀): 197, habitus; 198, head, dorsolateral; 199, antenna; 200, clava; 201, proximal part of forewing stalk; 202, forewing posterobasal marginal setae. 203–205, *Archaeromma senonicum* (paratype ♀): 203, head, ventrolateral; 204, antenna; 205, forewing.



Figs 206–212. 206, *Archaeromma masneri* (holotype ♀). 207–210, *Palaeomymar succini*: 207, habitus (neotype ♂); 208, forewing posterobasal marginal setae (neotype ♂); 209, ♀ forewing posterobasal marginal setae (ZMUC: 16-1/1961); 210, foreleg (neotype ♂). 211 and 212, ? *Mymaromella* sp. ♀ (ZMUC: 17-5/1963): 211, forewings; 212, calcar.



Figs 213–219. 213, *Galloromma* sp. ♀, head, dorsal (GPPC: HY17A). 214–217, *Galloromma bezomaisensis* (holotype): 214, antenna, dorsal; 215, lateral habitus reproduced from Schlüter (1978); 216, forewing posterobasal marginal setae and antennal funicle; 217, head, dorsal. 218 and 219, head and antennae of *Serphites* sp.: 218, lateral (MCZ: 5330); 219, frontal (PIN: 3730/28-30).



Figs 220–227. 220–222, *Serphites* sp. (PIN: 3730/31): 220, mesosoma, lateral; 221, pronotum-mesopectus; 222, mesosoma, ventrolateral. 223, *Serphites* sp. ♂ (MCZ: 5343), apex of gaster. 224 and 225, *Serphites* sp., gaster: 224, ventrolateral (PIN: 3730/28-30); 225, lateral (MCZ: 5330). 226, *Serphites* sp., forewing venation (MCZ: 5530). 227, forewing of undescribed representative of Scelionidae (PIN: 4703/10).

## Szépligeti's *Cyclaulax* types Deposited in the Hungarian Natural History Museum (Hymenoptera: Braconidae: Braconinae)

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**Abstract.**—The nine *Cyclaulax* species represented by types and deposited in the Museum Budapest as well as the type-species of the genus *Cyclaulax grandiceps* Cameron, housed in the Natural History Museum, London, are re-described and an identification key to the ten species is presented. Currently 11 *Cyclaulax* species are listed from the Neotropical Region. With 94 original figures.

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The genus *Cyclaulax* was created by Cameron (1911) on the basis of the new species, *C. grandiceps* Cameron from Guiana (former British Guiana). The first *Cyclaulax* species, however, were discovered by Szépligeti, who described a total of nine species originally ranged in the genus *Bracon* Fabricius (Szépligeti 1902, 1904, 1906). *Cyclaulax* belongs to the *Compsobracon* Ashmead group of genera (Quicke 1997, Leathers et al. 2005), its generic characters are listed below.

Quicke (1991) reviewed the non-European species of the subfamily Braconinae deposited in the Hungarian Natural History Museum (=Magyar Természettudományi Múzeum), Budapest and he was the first who recognized the true taxonomic position of these nine *Bracon* species (enumerated below).

In the present paper the nine *Cyclaulax* species by Szépligeti as well as the generic type-species *C. grandiceps* are re-described and an identification key compiled for the ten species to promote their reliable recognition. Quicke (1997: 152) indicated that *Cyclaulax* specimens are "frequently collected" in the Neotropical Region. The number of the *Cyclaulax* species, consequently, will considerably increase as a result of future taxonomic research.

Our knowledge of the Braconinae wasps of the Neotropical Region is less advanced. In this respect it is worthwhile to quote Quicke's (1997) assertions: "Comparatively few studies have been made on the New World fauna since the first two decades of this century." and "Undoubtedly, difficulties in identifying New World braconines in general and Neotropical species in particular have hampered and even discouraged work on their biology and hence possible use in biological or integrated control programs." The present contribution is a slight step towards the promotion of our improved knowledge of the Neotropical braconines.

### METHODS

**Abbreviations.**—The following abbreviations are applied in the re-descriptions of the species and in the identification key to *Cyclaulax* species (after van Achterberg 1993: 4–5):

**Eye:** OOL = ocellar-ocular line, i.e. shortest distance between hind ocellus and compound eye; POL = postocellar line, i.e. shortest distance between hind two ocelli.

**Fore wing:** *m-cu* = recurrent vein; *r* = first section of the radial vein; *1-M* = basal vein; *2-Cu1* = second section of the discal vein; *2-SR* = first transverse cubital vein;



3-SR = second section of the radial vein;  
SR1 = third section of the radial vein; 1-SR+M = first section of the cubital vein.

**Hind wing:** *cu-a* = nervellus.

## TAXONOMY

### Genus *Cyclaulax* Cameron

*Cyclaulax* Cameron, 1911: 7, type species: *Cyclaulax grandiceps* Cameron, 1911. – Quicke 1989: 119 (taxonomy), 1997: 152 (in key).

*Generic features of Cyclaulax.*—(1) Face sculptured as in Figs 30–33 (Quicke 1997: 163), otherwise head and mesosoma polished. (2) Every tergite polished, second tergite antero-medially without an area bordered by furrow or not “pinched up”; third tergite usually clearly longer than second tergite (Figs 7, 23, 49, 75). (3) Basitarsus of fore leg laterally compressed or flattened (Figs 42, 63, 72). (4) Suture between tergites 2–3 trisinate, median sinuation deeply curved (Figs 7, 23, 49, 75). (5) Venation of forewing as in Fig. 6 (Quicke 1997: 159), vein 1-SR+M distinctly bent. (6) Eye somewhat protruding (Figs 1, 19, 38, 89). (7) Hypopygium pointed, ovipositor sheath long (Fig. 50, 76).

With the help of Quicke’s key (1997) to the Nearctic–Neotropic genera of the subfamily Braconinae it is fairly easy to identify the genus *Cyclaulax*. The nearest genera to *Cyclaulax* are *Gracilibracon* Quicke, 1995 and *Cyclaulacidea* Quicke and Delobel, 1995.

*Cyclaulax* species are distributed in the Neotropical Region except Chile. In the world catalogue of Braconidae (Shenefelt 1978: 1682) only one, the type species, is listed for this genus. Szépligeti has described nine species originally assigned to the genus *Bracon* (Szépligeti 1902, 1904, 1906). They were transferred to *Cyclaulax* by Quicke (1991) except *B. flexuosus* and *B. linurus* with the taxonomic note “Belongs to an undescribed genus of the *Campsobraconoides* (= *Campsobracon*) group.” I do not concur with this opinion, i.e. I consider

these two species as representing also the genus *Cyclaulax*.

The following nine *Cyclaulax* species by Szépligeti (represented by type material or named specimens) are housed in the Hungarian Natural History Museum: *Cyclaulax atriceps* (Szépligeti, 1904), *C. binotatus* (Szépligeti, 1904), *C. enotatus* (Szépligeti, 1904), *C. flexuosus* (Szépligeti, 1902), *C. linurus* (Szépligeti, 1906), *C. lunatus* (Szépligeti, 1906), *C. mesonurus* (Szépligeti, 1906), *C. paraguayensis* (Szépligeti, 1904) and *C. sicuaniensis* (Szépligeti, 1904).

By Mrs S. Lewis-Ryder’s (London) kind assistance I had the opportunity to study the type species (*C. grandiceps* Cameron) of the genus *Cyclaulax* Cameron. In the taxonomic part of the present article its redescription is given.

An eleventh species, *C. crassitarsis* (Brues, 1912), is listed in the checklist (see below).

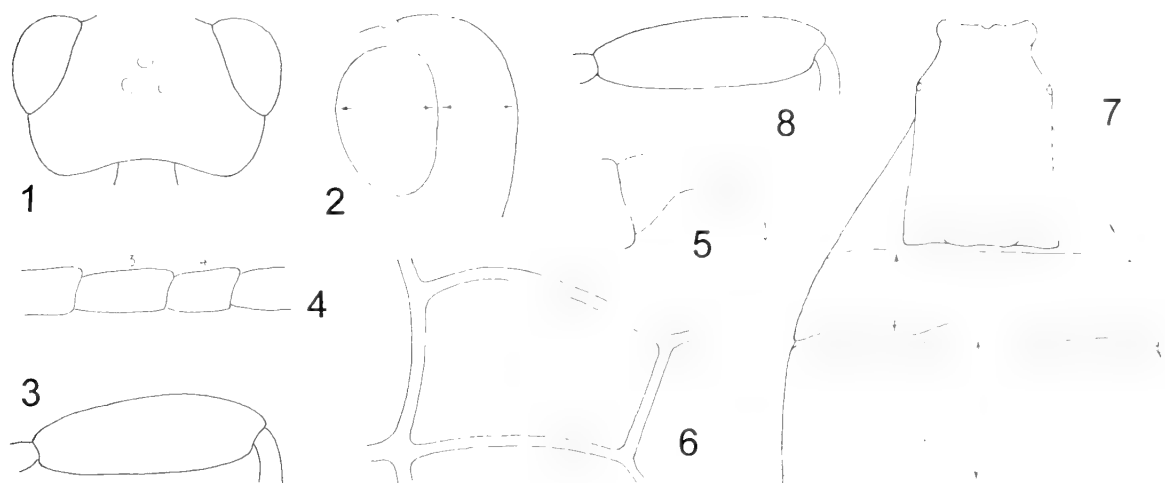
### *Cyclaulax atriceps* (Szépligeti) (Figs 1–8)

*Bracon atriceps* Szépligeti, 1904: 184 ♀, type locality: “Peru: Marcapata”, female holotype (designated by Papp in 1969) in Magyar Természettudományi Múzeum, Budapest; examined. – Szépligeti 1906: 591 (in key). Shenefelt 1978: 1467 (as *Bracon atriceps*, literature up to 1906). Quicke 1991: 171 (as *Cyclaulax atriceps* comb. n., type depository).

*Designation of the female holotype of Bracon atriceps.*—(first label, printed) “Marcapata / Peru”; second label is the holotype card, third label is with the inventory number 1549 (second and third labels were attached by me); fourth label is with the actual name *C. atriceps* (Szépligeti) given by Quicke in 1989.

*Redescription of the female holotype of Bracon atriceps.*—Body 8 mm long. Antenna somewhat shorter than body and with 41 antennomeres (left antenna; right flagellum deficient, i.e. with 21 flagellomeres). Scape in outer-lateral view twice as long dorsally as broad apically (cf. Fig. 60). – Head in





Figs 1–8. *Cyclaulax atriceps* (Szépligeti), female lectotype: 1 = head in dorsal view, 2 = head in lateral view, 3 = hind femur, 4 = tarsomeres 3–4 of fore leg, 5 = claw, 6 = first discal cell of fore wing, 7 = tergites 1–3; female: 8 = hind femur

dorsal view (Fig. 1) less transverse, 1.7 times as broad as long, eye 1.5 times longer than temple, temple faintly receded. Eye in lateral view clearly 1.5 times as high as wide and 1.6 times wider than temple, latter evenly beyond eye (Fig. 2).

Mesosoma in lateral view 1.6 times as long as high. Hind femur 2.9 times as long as broad distally (Fig. 3). Fourth tarsomere of fore leg in lateral view 1.35 times as long as high (Fig. 4). Claw of hind leg as in Fig. 5. First discal cell high,  $1-M$  1.35 times as long as  $m-cu$ ,  $1-M$  bent, veins relatively thick (Fig. 6). – First tergite 1.4 times as long as broad behind, its scutum rather narrow; third tergite 1.6 times as long medially as second tergite laterally, suture between them less strongly trisinate (Fig. 7, see arrows). Ovipositor sheath as long as hind tibia + tarsus combined.

Head and mesosoma black, mesoscutum and scutellum anteriorly reddish. Tergites 1–2 reddish, further tergi blackish to black. Legs black. Wings brown fumous, veins brown,  $1-SR+M$  yellowish.

Deviating features of two females (from the locality “Peru, Pachitea”). – Body 9 mm long. Both flagelli deficient. Head in dorsal view 1.6 times as broad as long (1 ♀). Hind femur 3.1 times as long as broad distally (Fig. 8).

Deviating features of one female (from the locality “Peru, Pachitea”). – Body 9 mm long. Both flagelli deficient. A light coloured (or albanic) specimen: mesoscutum, scutellum, tegula, upper fourth of mesopleuron and lateral corner of pronotum reddish yellow; fore leg: coxa, trochanters and tarsus yellowish, femur + tibia + fifth tarsomere dark brown.

Male and host unknown.

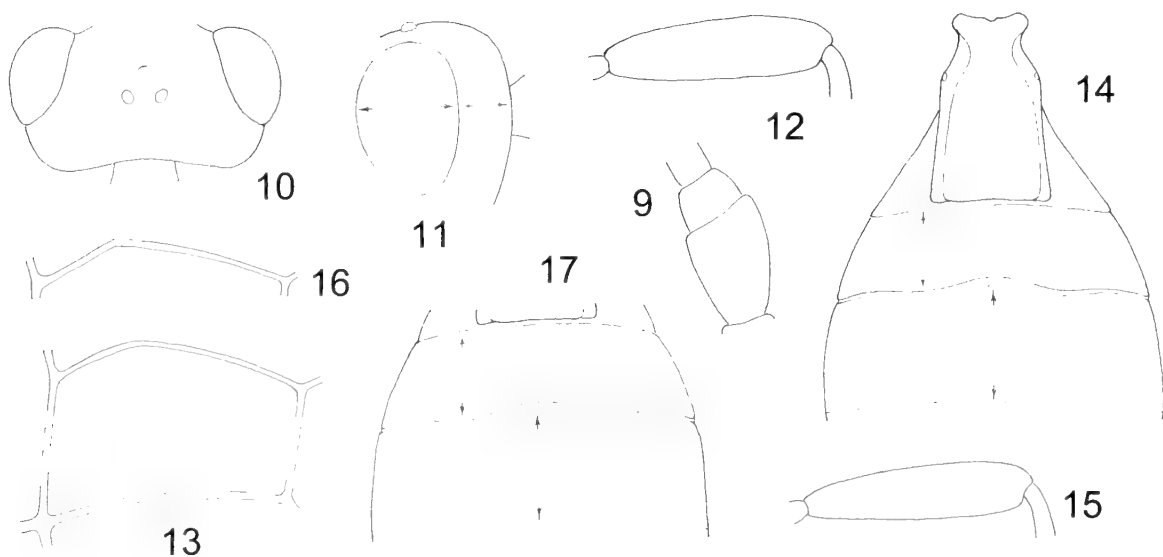
*Distribution*.—Peru.

*Taxonomic position*.—*C. atriceps* is closest to *C. enotatus*, their specific distinction is presented in the key-couplets 19(20) – 20(19).

### *Cyclaulax binotatus* (Szépligeti) (Figs 9–17)

*Bracon binotatus* Szépligeti, 1904: 184 (description) and 186 (in key) ♀, type locality: “Peru: Marcapata”, female lectotype (+ six female paralectotypes designated by Papp in 1969, see Shenefelt l.c.) in Magyar Természettudományi Múzeum, Budapest; examined. – Szépligeti 1906: 590 (in key). Shenefelt 1978: 1470 (as *Bracon binotatus*, literature up to 1906). Quicke 1991: 171 (as *Cyclaulax binotatus* comb. n., type depository).

*Type designation of Bracon binotatus*.—Designation of the female lectotype: (first



Figs 9–17. *Cyclaulax binotatus* (Szépligeti), female lectotype: 9 = scape in outer-lateral view, 10 = head in dorsal view, 11 = head in lateral view, 12 = hind femur, 13 = first discal cell of fore wing, 14 = tergites 1–3; female paralectotype: 15 = hind femur, 16 = vein 1–SR–M of fore wing, 17 = tergites 2–3

label, printed) “Marcapata / Peru”; Second label is the lectotype card, third label is with the inventory number 1542 (second and third labels were attached by me); fourth label is with the actual name *C. binotatus* given by Quicke in 1989. – Lectotype is in good condition: (1) micropinned; (2) left flagellum distally deficient, i.e. with 22 flagellomeres; (3) fore right wing basally torn.

*Designation of the six female paralectotypes.*—(first label, printed) “Marcapata / Peru”; second label is the lectotype card, third label is with the inventory numbers 1543–1548 (second and third labels were attached by me); fourth label is with the actual name *C. binotatus* given by Quicke in 1989. – Paralectotypes are in fairly good condition: micropinned, flagelli partly or entirely deficient.

*Taxonomic remark.*—Quicke (1991: 171) correctly indicated that the “specimens 1545–1548 inclusive appear to belong to a different species from specimens 1542–1544”. – The lectotype (no. 1542) and one female paralectotype (no. 1544) are representing the nominate form *Bracon binotatus* (albeit the paralectotype is “var. ♀” by Szépligeti l.c.). – One female paralectotype

(no. 1543) is near to *C. sicuaniensis* (Szépligeti) and supposedly representing a new *Cyclaulax* species (specimen in question is in poor condition, inappropriate for type designation). – Two female paralectotypes (nos 1545, 1547) are “var. 2. ♀” by Szépligeti (l.c.) and received the new name *C. lunatus* (Szépligeti) by me. – One female paralectotype (no. 1546) is in the Nationaal Natuurhistorisch Museum, Leiden and one female paralectotype (no. 1548) is in the Zoological Institute, Saint Petersburg as exchange material. The female paralectotype in Leiden does not represent the species *C. binotatus* (Szépligeti) and is near to *C. lunatus* (Szépligeti), however, deviating from it by the following features: first tergum less broad, head rather subcubic, fore leg entirely and tarsus of middle leg yellow; perhaps it will prove to be a new *Cyclaulax* species (both its flagelli missing), further specimens are needed to detect its true taxonomic status.

The true *Cyclaulax binotatus* (Szépligeti), represented by the female lectotype, one female paralectotype and one female (without type status), deviates from all other *Cyclaulax* species of Szépligeti in that its scape is not emarginated apically neither in

its outer- (Fig. 9) nor in its inner-lateral view. This feature combined with the very wide scutum of first tergite (Fig. 14) may serve in the future either for subgeneric separation within the genus *Cyclaulax* or to create a new genus. Again, more material is needed to decide this taxonomic problem.

*Redescription of the female lectotype of Bracon binotatus.*—Body 7.2 mm long. Antenna about as long as body and with 43 antennomeres (left flagellum deficient). Scape in outer-lateral view 1.6 times as long dorsally as broad apically (Fig. 9). – Head in dorsal view (Fig. 10) transverse, almost 1.9 times as broad as long, temple constricted, eye clearly twice as long as temple. Eye in lateral view 1.5 times as high as wide and clearly two times wider than temple (Fig. 11).

Mesosoma in lateral view 1.5 times as long as high. Hind femur 3.6 times as long as broad distally (Fig. 12). First discal cell less high, 1–M 1.3 times as long as *m-cu*, 1–M straight, 1–SR+M broken in its run (Fig. 13). – First tergite 1.55 times as long as broad behind, its lateral part narrow, suture between tergites 2–3 weakly trisinate; third tergite somewhat more than one-fifth longer medially than second tergite laterally (Fig. 14, see arrows). Ovipositor sheath as long as hind tibia + tarsus combined.

Scape black, flagellum blackish. Head yellow, frons, vertex and face medially black, face below antennal socket pale yellow. Palpi yellow. Mesosoma reddish yellow, propodeum + metapleuron blackish brown. Tergites black; sternites ochreous, medio-longitudinally with a black streak. Fore leg yellow with faint brownish tint, middle and hind legs blackish brown. Wings brownish fumous, pterostigma and veins dark brown to brown.

Deviating features of one female paralectotype and one female. – Similar to the female lectotype. Body 6.5–7 mm long. Antenna with 46 antennomeres (paralectotype). Hind femur four times as long as

broad somewhat distally (Fig. 15). Vein 1–SR+M of first discal cell broken angularly (Fig. 16). First tergite 1.6 times as long as broad behind. Third tergite one-fifth longer than second tergite (Fig. 17). Face below antennal socket entirely black (i.e. without yellow macula, female paralectotype) or face almost entirely reddish yellow (one female).

Male and host unknown.

*Distribution.*—Peru.

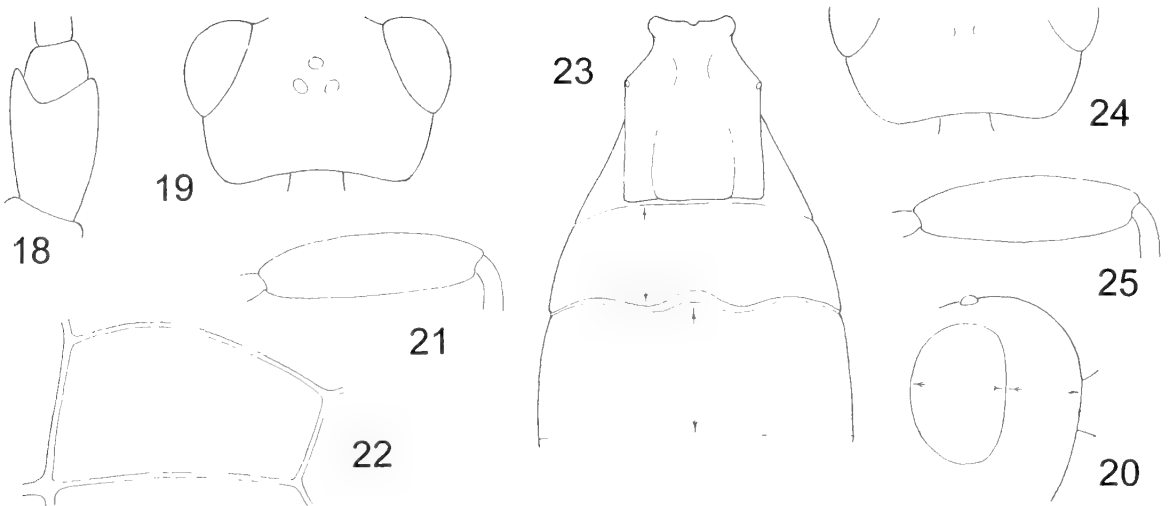
*Taxonomic position.*—*C. binotatus* stands alone with its clearly transverse head and constricted temple, see key-couplets 7(8) – 8(7).

### *Cyclaulax enotatus* (Szépligeti) (Figs 18–25)

*Bracon enotatus* Szépligeti, 1904: 184 ♀, type locality: "Peru: Marcapata", female lectotype (and three female paralectotypes designated by Papp in 1969, see Shenefelt l.c.) in Magyar Természettudományi Múzeum, Budapest; examined. – Szépligeti 1906: 591 (in key). Shenefelt 1978: 1481 (as *Bracon enotatus*, literature up to 1906). Quicke 1991: 171 (as *Cyclaulax enotatus* comb. n., type depositary).

*Type designation of Bracon enotatus.*—Designation of the female lectotype and two female paralectotypes (as "var. ♀" in Szépligeti l.c.): (first label, printed) "Marcapata / Peru"; second label is the lectotype and paralectotype cards, third label is with the inventory number 1551 (lectotype) and 1552–1553 (paralectotypes) (second and third labels attached by me); fourth label is with the actual name *C. enotatus* given by Quicke in 1989. – Lectotype is in rather poor condition: (1) pinned by mesosoma; (2) both flagelli missing; (3) right hind leg (except coxa + trochanters) glued on a separate card, tarsomeres 2–5 of right middle leg missing; (4) right fore wing also glued on a separate card.

*Designation of one female paralectotype.*—(first label, printed) "Peru / Chanchalmajo"; second label is the paralectotype card, third label is with the inventory



Figs 18–25. *Cyclusax enotatus* (Szépligeti), female lectotype: 18 = scape in outer-lateral view, 19 = head in dorsal view, 20 = head in lateral view, 21 = hind femur, 22 = first discal cell of fore wing, 23 = tergites 1–3; female paralectotype: 24 = temple in dorsal view, 25 = hind femur

number 1552 (both labels attached by me); fourth label is with the actual name *C. enotatus* (Szépligeti) given by me. – The three paralectotypes are also in poor condition: (1) pinned by mesosoma; (2) flagelli either missing or deficient; (3) legs partly missing.

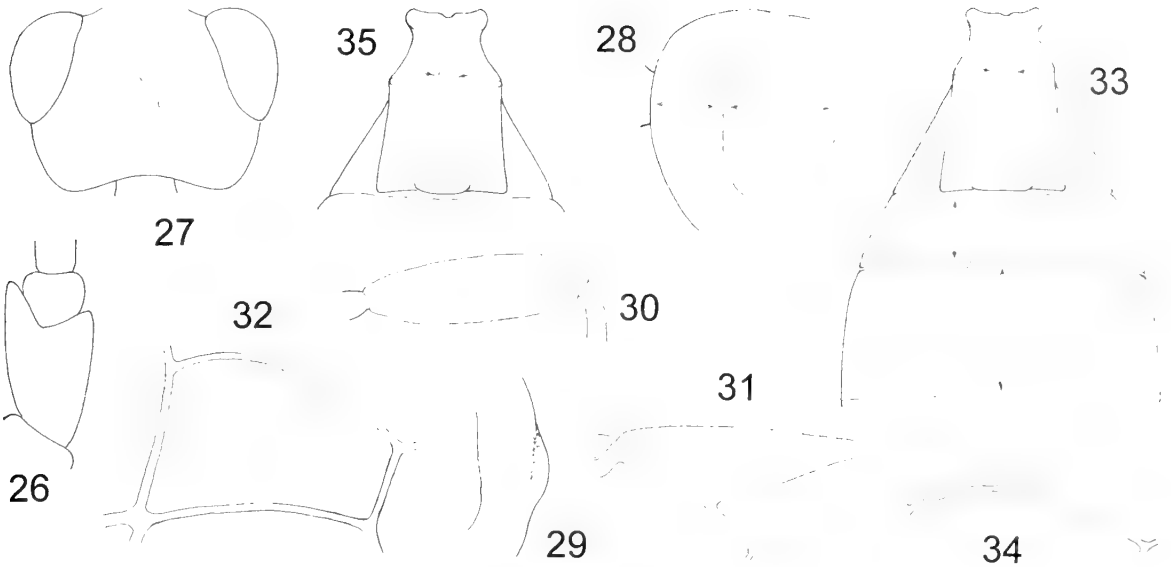
*Taxonomic remark.*—The two female paralectotype (“var. ♀” by Szépligeti, from Peru: Marcapata) do not represent *C. enotatus*, they belong to *C. lunatus* (Szépligeti) and I labelled them accordingly. One female paralectotype is in Museum Budapest and one female paralectotype is in Museum Leiden (as exchange material). – The third female paralectotype, from Peru: Chanchalmajo, is a true *C. enotatus* and is in the Museum Budapest.

*Redescription of the female lectotype of Bracon enotatus.*—Body 8 mm long. Scape in outer-lateral view 1.7 times as long dorsally as broad apically (Fig. 18). Both flagelli missing. – Head in dorsal view (Fig. 19) transverse, 1.6 times as broad as long, temple narrowing, eye almost 1.5 times (or clearly one-third) longer than temple. Eye in lateral view 1.5 times as high as wide and 1.3 times wider than temple, temple beyond eye evenly broad (Fig. 20).

Mesosoma in lateral view 1.75 times as long as high. Hind femur 3.6 times as long as broad medially (Fig. 21). First discal cell less high, 1–M nearly 1.6 times as long as *m-cu*, 1–M straight (Fig. 22). – First tergite 1.2 times as long as broad behind, scutum of tergite wide; second tergite less short, third tergite nearly 1.4 times as long medially as second tergite laterally (Fig. 23, see arrows). Suture between tergites 2–3 trisinate (Fig. 23). Ovipositor sheath nearly as long as hind tibia + tarsus combined.

Scape, pedicel, head, legs and tergi black. Palpi dark brown, its ultimate joint light brown. Mesosoma testaceous; propodeum, metapleuron and mesosternum black. Tegula also testaceous. Fore coxa yellowish. Wings brownish fumous, pterostigma and veins brown.

*Deviating features of one female paralectotype of Bracon enotatus (locality: Peru, Chanchalmajo).*—Similar to the female lectotype. Body 9 mm long. Both flagelli deficient, right flagellum with 28 and left flagellum with 7 flagellomeres. First flagellomere 1.4 times and 28th flagellomere cubic, i.e. as long as broad. Temple in dorsal view somewhat more narrowing (Fig. 24). Hind femur 3.3 times as long as



Figs 26–35. *Cyclaulax flexuosus* (Szépligeti), female lectotype: 26 = scape in outer-lateral view, 27 = head in dorsal view, 28 = head in lateral view, 29 = lump of left temple in lateral view, 30 = hind femur, 31 = pterostigma and vein *r* of fore wing, 32 = first discal cell of fore wing, 33 = tergites 1–3; male paralectotype: 34 = vein 1–SR–M of fore wing, 35 = first tergite

broad medially (Fig. 25). Cheek yellow. Mesosternum testaceous.

Male and host unknown.

*Distribution*.—Peru.

*Taxonomic position*.—*C. enotatus* is nearest to *C. atriceps* (Szépligeti), the distinction is presented in key-couplets 19(20)–20(19).

*Cycaulax flexuosus* (Szépligeti)  
(Figs 26–35)

*Bracon flexuosus* Szépligeti, 1902: 42 ♂, type locality: “Venezuela: Merida”, male lectotype (and one male paralectotype, designated by Papp in 1969) in Magyar Természettudományi Múzeum, Budapest; examined. – Szépligeti 1904: 187 (in key), 1906: 591 (in key). Shenefelt 1978: 1485 (as *Bracon flexuosus*, literature up to 1906). Quicke 1991: 172 (type depository).

*Type designation of Bracon flexuosus*.—Designation of the male lectotype: (first label) “Merida” (printed) / “Venezuela” (L. Biró’s manuscript); (second label) “Br. flexuosus” (Szépligeti’s manuscript) / “det. Szépligeti” (printed); third label is my lectotype card, fourth label is with the inventory number 1560 (third and fourth

labels were attached by me); fifth label is with the actual name *C. flexuosus* given by me. – Lectotype is in good condition: (1) pinned by mesosoma; (2) left flagellum missing, right flagellum deficient.

Designation of the male paralectotype: (first label) “Merida” (printed) / “Venezuela” (L. Biró’s manuscript); second label is with the paralectotype card, third label is with the inventory number 1561 (second and third labels were attached by me); fourth label is with the actual name *C. flexuosus* given by me. – Paralectotype is in fairly good condition: (1) pinned by mesosoma; (2) both flagelli distally deficient; (3) left pair of wings missing.

*Redescription of the male lectotype of Bracon flexuosus*.—Body 7.5 mm long. Right flagellum with 33 flagellomeres (left flagellum missing). Scape in outer-lateral view almost 1.6 times as long dorsally as broad apically, deeply emargined, ventrally as long as dorsally (Fig. 26). First flagellomere twice and 33rd flagellomere subcubic, i.e. a bit longer than broad. – Head in dorsal view (Fig. 27) subcubic, 1.5 times as broad as long, eye 1.66 times length of temple, temple moderately rounded. Eye in lateral

view almost 1.5 times as high as wide and 1.6 times wider than temple, latter ventrally narrowing (Fig. 28, see arrows). Left temple ventrally with a (teratological?) small lamp (Fig. 29).

Mesosoma in lateral view almost twice as long as high. Hind femur less broadening distally, 3.3 times as long as broad medially (Fig. 30). Vein *r* of fore wing clearly longer than half width of pterostigma (Fig. 31). First discal cell high, 1-*M* weakly bent and 1.7 times as long as *m-cu* (Fig. 32). – First tergite 1.4 times as long as broad behind, its scutum more narrowing anteriorly; third tergite 1.7 times longer medially than second tergite laterally (Fig. 33, see arrows), suture between tergites 2–3 weakly trisinate (Fig. 33).

Scape and pedicel rusty brown, flagellum dark brown. Head, mesosoma and legs rusty brown; mesosoma testaceous, apically blackish. Palpi light brown to brown. Tegula rusty brown. Fore tarsus yellow. Wings brown fumous, pterostigma brown, vein brown to light brown.

*Redescription of the male paralectotype of Bracon flexuosus.*—Similar to the male lectotype. Body 6 mm long. Both flagelli distally deficient: right flagellum with 17 and left flagellum with 14 flagellomeres. Vein 1-SR-M of first discal cell slightly less bent (Fig. 34). First tergite clearly 1.3 times as long as broad behind, its scutum somewhat narrowing (Fig. 35).

Female and host unknown.

*Distribution.*—Venezuela.

*Taxonomic position.*—*C. flexuosus* is nearest to *C. paraguayensis* (Szépligeti) and to *C. sicuaninensis* (Szépligeti), their distinction is presented in the key-couplets 14(15) – 17(16).

### *Cyclaulax grandiceps* Cameron (Figs 36–50)

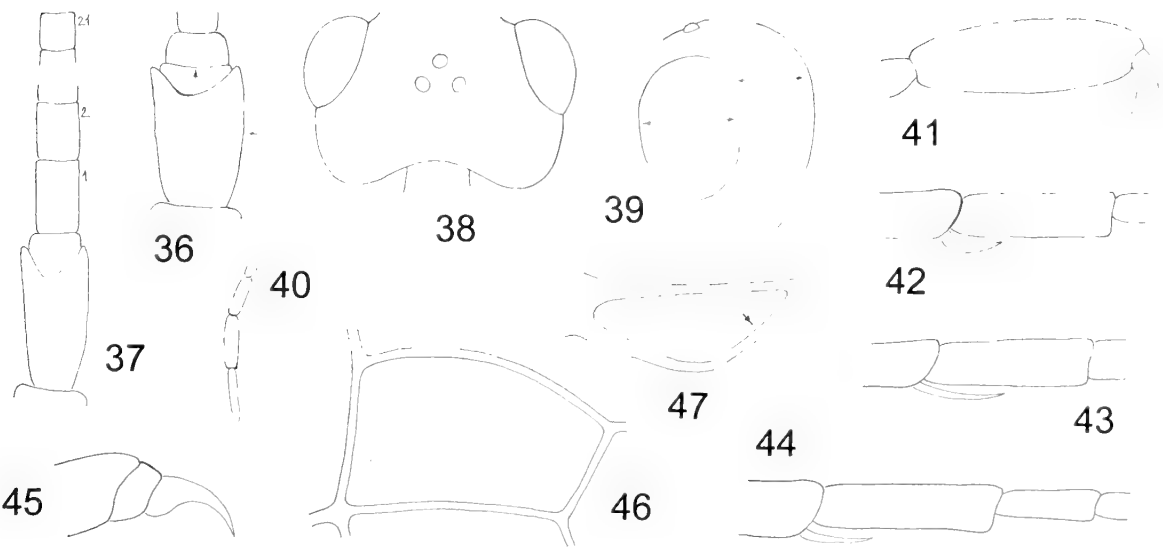
*Cyclaulax grandiceps* Cameron, 1911: 7 ♀ (syntype series one female), type locality: British Guiana, female holotype (=“Type”) in The Natural History Museum, London; examined. – Shenefelt 1978: 1682 (as *Cyclaulax grandiceps*, literature up to 1911).

*Designation of the female holotype* (=“Type”) of *Cyclaulax grandiceps*.—(first round label with red frame) “Type” (printed); (second label) “B. M. Type Hym.” (printed) “3.c.152” (handscript); (third great label with Cameron’s handscript) “*Cyclaulax* / *grandiceps* / Cam. Type / Br. Guyana”; (fourth label, printed) “P. Cameron Coll. 1914–110.” – The holotype is in fairly poor condition: (1) pinned by mesosoma; (2) left flagellum missing, right flagellum deficient; (3) left fore wing missing, right fore wing glued separately on a small card; (4) right fore leg stuck to right mesopleuron; (5) missing: tarsi of left fore and left hind legs, fifth tarsomere of right fore tarsus and tarsomeres 2–5 of right middle tarsus.

*Redescription of the female holotype of Cyclaulax grandiceps.*—Body 12 mm long. Scape cylindrical, in outer-lateral view twice as long dorsally (Fig. 36, see horizontal arrow) as broad apically, ventrally and dorsally of equal length, its outer side deeply emargined (Fig. 37), its inner side with an apico-median ledge (Fig. 36, see vertical arrow); pedicel short. Right flagellum deficient, i.e. with 21 flagellomeres. First flagellomere 1.5 times, second flagellomere 1.2 times as long as broad apically, further flagellomeres cubic (Fig. 37). – Head in dorsal view (Fig. 38) less transverse, 1.6 times as broad as long, eye somewhat protruding and almost 1.4 times length of temple, temple moderately rounded, occiput excavated. Ocelli near to each other, OOL three times as long as POL. Eye in lateral view 1.5 times as high as wide, one-third wider than temple medially, temple ventrally narrowing (Fig. 39, see arrows). Face with similar sculpture to that of Fig. 32 (cf. Quicke 1997: 163); otherwise head polished. Fourth maxillar palpal joint somewhat thicker and shorter than fifth joint (Fig. 40).

Mesosoma in lateral view almost twice as long as high, polished. Notaulix distinct weakly. Propodeum polished. – Hind femur three times as long as broad distally

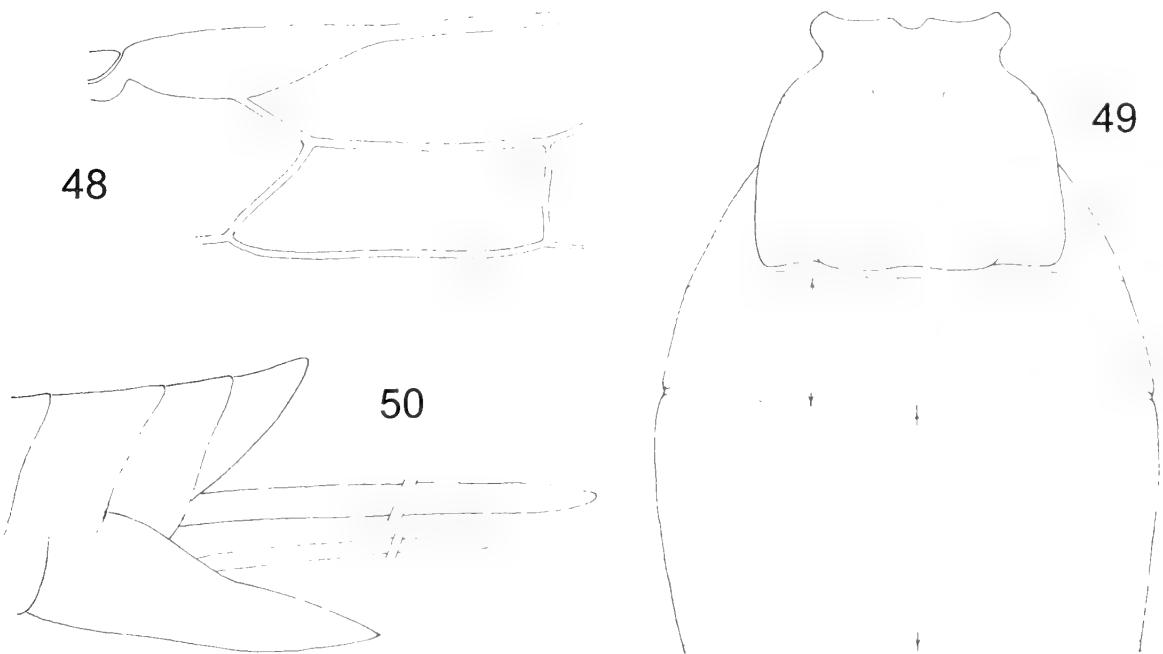




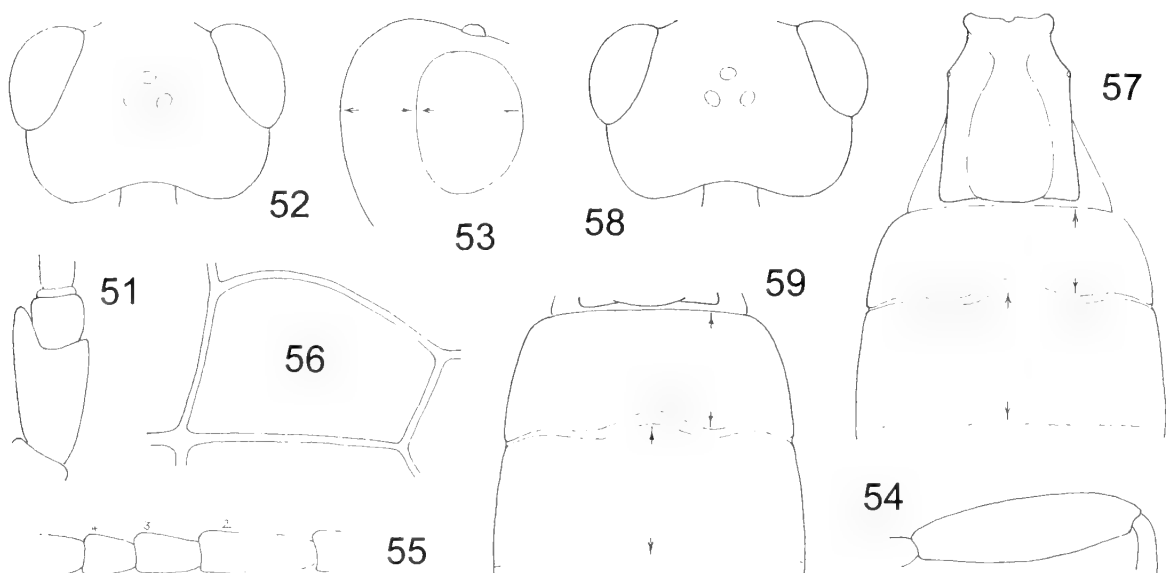
Figs 36–47. *Cycloaulax grandiceps* Cameron, holotype: 36 = scape in outer-lateral view, 37 = scape in inner-lateral view and flagellomeres 1–2 + 21, 38 = head in dorsal view, 39 = head in lateral view, 40 = maxillar palpal joints 3–5, 41 = hind femur, 42 = basitarsus + spur of fore leg, 43 = basitarsus + spur of middle leg, 44 = basitarsus, spur and second flagellomere of hind leg, 45 = claw, 46 = first discal cell of fore wing, 47 = subbasal cell with vein *cu-a* of hind wing

(Fig. 41). Inner spur of middle tibia slightly longer than (Fig. 43) and that of hind tibia less than half as long as basitarsus, latter somewhat thick (Fig. 44). Claw curved, basally widening (Fig. 45).

Fore wing as long as body. Pterostigma (Fig. 48) 3.6 times as long as wide and issuing *r* proximally from its middle, *r* as long as width of pterostigma. Second submarginal cell long, 3–SR almost twice



Figs 48–50. *Cycloaulax grandiceps* Cameron, holotype: 48 = pterostigma and first submarginal cell of fore wing, 49 = tergites 1–3, 50 = posterior end of metasoma with hypopygium and ovipositor apparatus



Figs 51–59. *Cyclaulax linurus* (Szépligeti), female lectotype: 51 = scape in outer-lateral view, 52 = head in dorsal view, 53 = head in lateral view, 54 = hind femur, 55 = tarsomeres 2–4 of fore leg, 56 = first discal cell of fore wing, 57 = tergites 1–3; female paralectotype: 58 = head in dorsal view, 59 = tergites 2–3

as long as 2–SR, SR1 straight, somewhat longer than 3–SR and reaching tip of wing. First discal cell less high, 1–M 1.5 times length of *m-cu*, 1–SR+M clearly bent (Fig. 46). – Hind wing: *cu-a* as in Fig. 47 (see arrow).

First tergite (Fig. 49) somewhat broader behind than long, scutum convex, lateral part of tergite fairly wide. Second tergite transverse, 3.4 times as broad behind as long laterally; third tergite 1.8 times longer medially than second tergite laterally (Fig. 49, see arrows); suture between them deep, smooth, trisinate, median sinuation the deepest (Fig 9). Every tergite polished. Hypopygium pointed, ovipositor sheath long, as long as hind femur + tibia + tarsomeres 1–2 combined (Fig. 50).

Ground colour of body reddish yellow. Head and antenna black, flagellum with very weak brownish suffusion. Labrum and cheek ferruginous, palpi blackish brown to brown. Pronotum and -sternum black to blackish. Last two metasomal segments black. Legs black, fore coxa + trochanters reddish yellow, tarsomeres of middle leg apically rusty. Wings dark brown fumous, pterostigma blackish, veins proximo-distally black to brown.

Male and host unknown.

*Distribution*.—Guiana

*Taxonomic position*.—*C. grandiceps* Cameron differs from all other *Cyclaulax* species by its very broad first tergite; *C. lunatus* (Szépligeti) and *C. paraguayensis* (Szépligeti) appear to be the nearest to *C. grandiceps* with their relatively broad first tergites; see also the key-couplets 1(6) – 5(4).

*Cyclaulax linurus* (Szépligeti) comb. n.  
(Figs 51–59)

*Bracon linurus* Szépligeti, 1906: 591 (in key) and 593 (description) ♀, type locality: "Bolivia: Mapiri", female lectotype (+ one female paralectotype, designated by Papp in 1969) in Magyar Természettudományi Múzeum, Budapest; examined. – Shenefelt 1978: 1503 (as *Bracon linurus*, literature up to 1906). Quicke 1991: 172 (taxonomy, type depository).

*Type designation of Bracon linurus*.—Designation of the female lectotype of: (first label, printed) "Bolivia / Mapiri"; second label is the lectotype card, third label is with the inventory number 993 (second and third labels were attached by me); fourth label is with the actual name *C.*

*linurus* (Szépligeti) given by me. – Lectotype is in fairly poor condition: (1) pinned by mesosoma; (2) both flagelli deficient distally; (3) right fore wing antero-medially damaged, distal third part of left fore wing glued on a separate small card; (4) left ovipositor sheath broken (present its short basal part); (5) head broken, glued to prosoma.

*Designation of the female paralectotype.*—(first label, printed) “Peru / Mercapata”; second label is the paralectotype card, third label is with the inventory number 994 (second and third labels were attached by me); fourth label is with the actual name *C. linurus* (Szépligeti) given by me. – Paralectotype is in fair condition: (1) micropinned by mesosoma; (2) both flagelli deficient distally; (3) right hind wing creased.

*Redescription of the female lectotype of Bracon linurus.*—Body 8 mm long. Scape in outer-lateral view 1.7 times as long dorsally as broad apically (Fig. 51). Both flagelli deficient, right flagellum with 27 and left flagellum with 18 flagellomeres. First flagellomere twice and 27th flagellomere subcubic, i.e. a bit longer than broad. – Head in dorsal view (Fig. 52) less transverse, clearly 1.5 times as broad as long, eye 1.4 times longer than temple, temple clearly rounded. Eye in lateral view 1.3 times as high as wide and twice wider than temple, latter beyond eye evenly broad (Fig. 53, see arrows).

Mesosoma in lateral view 1.6 times as long as high. Hind femur 3.6 times as long as broad distally (Fig. 54). Tarsomeres 2–4 of fore leg in lateral view short, third tarsomere 1.6 times as long as high and fourth tarsomere cubic, a bit longer than high distally (Fig. 55). First discal cell less high, 1–M 1.5 times as long as *m-cu*, 1–M just bent (Fig. 56). – First tergite clearly 1.3 times as long as broad behind, its scutum fairly wide, i.e. lateral margin of tergite less wide; third tergite 1.5 times as long medially as long second tergite laterally; suture between them medially deep

(Fig. 57, see arrows). Ovipositor sheath longer than body.

Ground colour of body black; legs also black, fore tarsus yellow, middle and hind tarsi dark brownish black. Scape and flagellum black. Mesoscutum, scutellum and tergites 1–2 testaceous. Wings brown fumous, pterostigma and veins dark brown to brown.

*Redescription of the female paralectotype of Bracon linurus.*—Similar to the female lectotype. Body 7.5 mm long. Head in dorsal view 1.5 times as broad as long, eye 1.3 times longer than temple, temple slightly less rounded (Fig. 58). Second tergite almost as long as third tergite (Fig. 59, see arrows). Pronotum and propodeum with reddish yellow suffusion, mesoscutum and scutellum reddish yellow.

Male and host unknown.

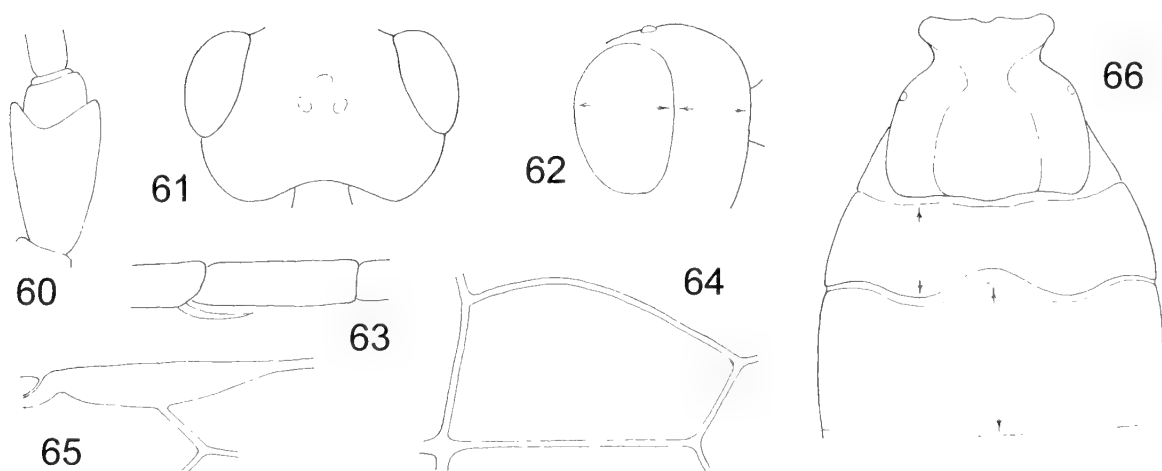
*Distribution.*—Bolivia, Peru.

*Taxonomic position.*—*C. linurus* is nearest to *C. mesonurus* (Szépligeti), their specific distinction is presented in the key-couplets 10(11) – 11(10).

### *Cyclaulax lunatus* (Szépligeti) (Figs 60–66)

*Bracon lunatus* Szépligeti, 1906: 591 (in key) and 594 (description) ♀, type locality: “Peru: Pachitea”, female lectotype (and three female paralectotypes, designated by Papp in 1969, see Shenefelt l.c.), in Magyar Természettudományi Múzeum, Budapest and one female paralectotype in Nationaal Natuurhistorisch Museum, Leiden as exchange. – Shenefelt 1978: 1504 (as *Bracon lunatus*, literature up to 1906). Quicke 1991: 172 (as *Cyclaulax lunatus* comb. n., type depository).

*Type designation of Bracon lunatus.*—Designation of the female lectotype: (first label, printed) “Peru / Pachitea”, second label is the lectotype card, third label is with the inventory number 1555 (second and third labels were attached by me); fourth label is with the actual name *Cyclaulax lunatus* (Szépligeti) given by Quicke in 1989. – Lectotype is in fairly good condition: (1) pinned by mesosoma; (2) right flagellum



Figs 60–66. *Cyclaulax lunatus* (Szépligeti): 60 = scape in outer-lateral view, 61 = head in dorsal view, 62 = head in lateral view, 63 = basitarsus and spur of middle leg, 64 = pterostigma and vein *r* of fore wing, 65 = first discal cell of fore wing, 66 = tergites 1–3

missing, left flagellum distally deficient; (3) right fore wing glued on a separate card.

*Designation of the four female paralectotypes*.—(three females in Budapest Museum, one female in Museum Leiden): (first label, printed) "Peru / Pachitea"; second label is the paralectotype card, third label is with the inventory numbers 1556–1558 (in Budapest); fourth (in Budapest) and third (in Leiden) labels is with the actual name *Cyclaulax lunatus* (Szépligeti) given by Quicke in 1989. – The four paralectotypes are in good condition: (1) pinned by mesosoma; (2) flagelli partly missing, partly deficient.

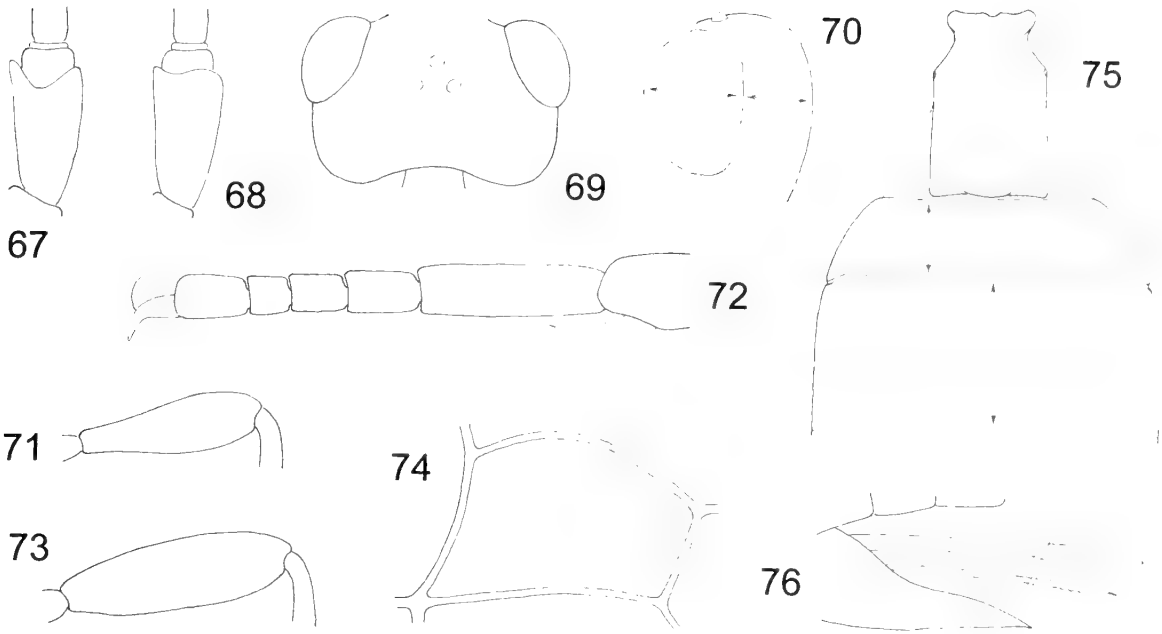
*Taxonomic rectification*.—Two female paralectotypes of *Bracon binotatus* Szépligeti (in Museum Budapest, Nos 1545 and 1547) and two female paralectotypes of *B. enotatus* var. ♀ (one female in Museum Budapest, No. 1553, one female in Museum Leiden) proved to belong to *B. lunatus* – now to the genus *Cyclaulax*. For further comments see "Taxonomic remarks" under these two species.

*Redescription of the female lectotype of Bracon lunatus*.—Body 10 mm long. Left flagellum broken distally, i.e. with 24 flagellomeres. Outer-lateral side of scape as in Fig. 60. First flagellomere 1.75 times and 24th flagellomere cubic, i.e. as long as

broad. – Head in dorsal view (Fig. 61) less transverse, nearly 1.6 times as broad as long, eye 1.7 times as long as temple, temple rounded. Eye in lateral view 1.6 times as high as wide and 1.46 times wider than temple, latter evenly broad beyond eye (Fig. 62).

Mesosoma in lateral view almost twice as long as high. Hind femur 3.1 times as long as broad medially. Inner spur of middle tibia shorter than half basitarsus (Fig. 63). Vein *r* somewhat longer than width of pterostigma and issuing from its middle (Fig. 65). First discal cell less high, 1–*M* 1.5 times as long as *m-cu*, 1–*M* straight and clearly not parallel with *m-cu*, 2–*Cu1* straight (Fig. 64). – First tergite as long as broad behind, broadest at its two-thirds, its scutum and lateral part fairly wide; suture between tergites 2–3 deep and trisinate; third tergite 1.65 times as long medially as long second tergite laterally (Fig. 66). Ovipositor sheath longer than hind tibia + tarsus combined.

Antenna blackish. Head black, median granulose field of face with luniform yellow macula, cheek also yellow, palpi brown. Ground colour of mesosoma testaceous, pronotum + prosternum and propodeum + metapleuron blackish to black. Fore leg rather dark brown, trochanters



Figs 67–76. *Cyclaulax mesonurus* (Szépligeti): 67 = scape in outer-lateral view, 68 = scape in inner-lateral view, 69 = head in dorsal view, 70 = head in lateral view, 71 = fore femur, 72 = tarsus of first leg, 73 = hind femur, 74 = first discal cell of fore wing, 75 = tergites 1–3, 76 = hypopygium and ovipositor apparatus

and tarsus with reddish suffusion. Middle and hind legs black to dark brown, middle tarsus faintly reddish. Tergites 1–3 reddish and laterally blackish to black, further tergites black. Wings brown fumous, pterostigma blackish brown, veins proximodistally blackish to light brown.

Deviating features of four paralectotypes of *B. lunatus*, (three female in Museum Budapest, one female in Museum Leiden, from Peru: Pachitea). Two female paralectotypes of *B. binotatus* var. ♀ Szépligeti (in Museum Budapest), two female paralectotypes of *B. enotatus* var. ♀ Szépligeti (one female in Museum Budapest, one female in Museum Leiden, from Peru: Marcapata) and one female (in Museum Leiden, from Peru: Pachytea) (the paralectotypes of *B. binotatus* and *B. enotatus* are representing *B. lunatus*, present rectification); total nine female specimens. – Similar to the female lectotype. Body 8–10 mm. Flagelli mainly distally deficient, rarely missing. Head in dorsal view 1.53–1.6 times as broad as long. Hind femur 3.1–3.5 times as long as broad medially. First tergite slightly broader

behind than long (2 ♀). Tergites 1–3 blackish with reddish suffusion (3 ♀).

Male and host unknown.

Distribution.—Peru.

Taxonomic position.—*C. lunatus* (Szépligeti) is nearest to *C. grandiceps* Cameron and *C. paraguayensis* (Szépligeti), their distinction is presented in the key-couplets 1(6) – 7(8).

*Cyclaulax mesonurus* (Szépligeti)  
(Figs 67–76)

*Bracon mesonurus* Szépligeti, 1906: 591 (in key) and 593 (description) ♀, type locality: “Bolivien: Mapiri”, female lectotype (designated by Papp in 1969) in Magyar Természettudományi Múzeum, Budapest; examined. – Shenefelt 1978: 1511 (as *Bracon mesonurus*, literature up to 1906). Quicke 1991: 172 (as *Cyclaulax mesonurus* comb. n., type depository).

Designation of the female holotype of *Bracon mesonurus*.—(first label, printed) “Bolivia / Mapiri”; second label is the lectotype card, third label is with the inventory number 1541 (second and third labels were attached by me), fourth label is

with the actual name *Cyclaulax mesonurus* (Szépligeti) given by Quicke in 1989. – Holotype is in good condition: (1) pinned by the mesosoma; (2) both flagelli deficient distally; (3) tarsus of left fore leg missing; (4) damaged: distal end of costal-subcostal vein (proximal from pterostigma) of right fore wing, membrane between median ( $M + Cu1$ ) and anal veins ( $1-1A$ ) of left fore wing longitudinally (i.e. parallel with these two veins) splitted.

*Redescription of the female holotype of Bracon mesonurus.*—Body 9 mm long. Scape in outer-lateral view just less than 1.9 times as long as broad apically (Fig. 67), in inner-lateral view as in Fig. 68. Both flagelli deficient, right flagellum with 25 and left flagellum with 14 flagellomeres. First flagellomere almost 1.5 times as long as broad and 25th flagellomere cubic, i.e. just broader than long. – Head in dorsal view (Fig. 69) less transverse, 1.57 times as broad as long, eye 1.37 times as long as temple, temple moderately rounded. Eye in lateral view 1.5 times as high as wide and 1.4 times wider than temple, latter beyond eye faintly narrowing ventrally (Fig. 70).

Mesosoma in lateral view twice as long as high. Fore femur 3.2 times as long as broad distally (Fig. 71). Tarsomeres 2–4 of fore leg in lateral view short, third tarsomere 1.36 times as long as high apically and fourth tarsomere cubic (Fig. 72). Hind femur 3.1 times as long as broad distally (Fig. 73). Inner spur of middle tibia shorter than half length of basitarsus (cf. Fig. 42). – First discal cell less high,  $1-M$  1.5 times as long as  $m-cu$ ,  $1-M$  bent,  $1-SR+M$  and  $2Cu1$  equal in length (Fig. 74). – First tergite clearly 1.5 times as long as broad behind, scutum narrow, i.e. lateral part of tergite wide; third tergite medially nearly twice as long as second tergite laterally; suture between them less trisinate and less deep (Fig. 75). Hypopygium pointed, ovipositor sheath somewhat longer than hind tibia + tarsus combined (Fig. 76).

Scape black, pedicel + flagellum brownish black. Head black, palpi dark brown.

Mesosoma testaceous; blackish to black: prosoma, propodeum and metapleuron. Tegula testaceous. Tergites 1–3 reddish yellow, rest of tergites blackish to black. Legs black; fore tibia brownish yellow, fore tarsus yellow, middle tibia brown, middle tarsus yellow, hind tibia + tarsus brownish black. Wings brown fumous, pterostigma dark brown, veins brown to light brown.

Male and host unknown.

*Distribution.*—Bolivia.

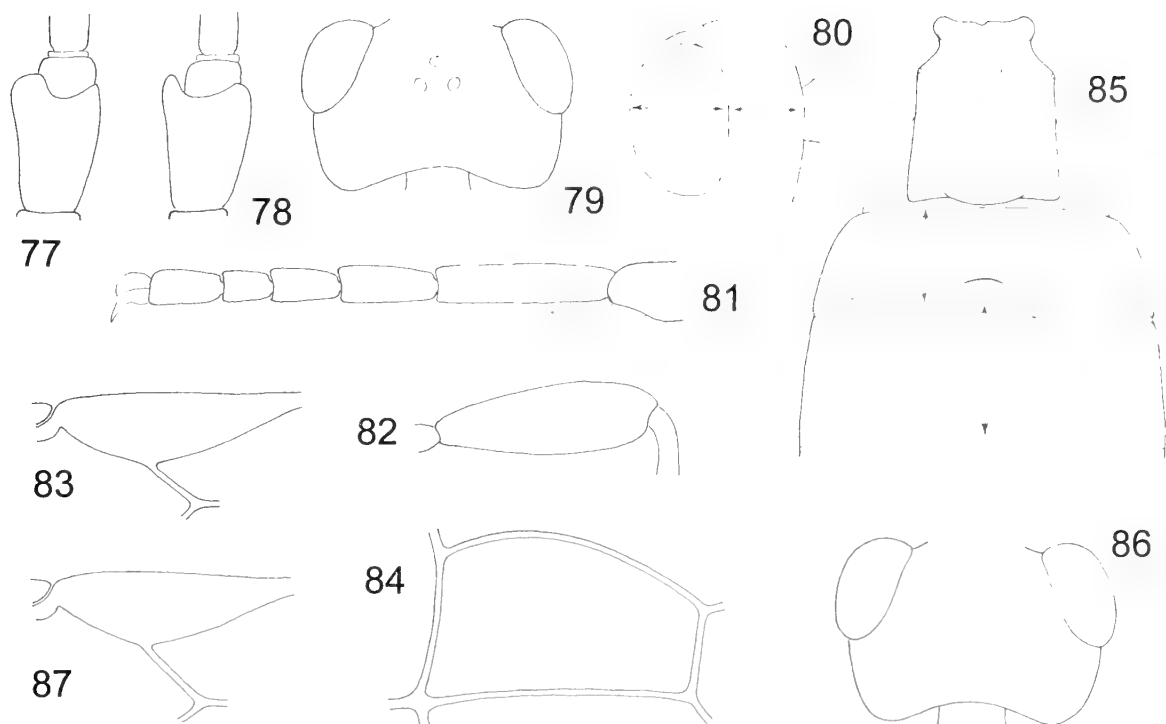
*Taxonomic position.*—*C. mesonurus* (Szépligeti) is nearest to *C. linurus* (Szépligeti), their distinction is in key-couplets 10(11) – 11(10).

### *Cyclaulax paraguayensis* (Szépligeti) (Figs 77–87)

*Bracon paraguayensis* Szépligeti, 1914: 184 ♀, type locality: "Paraguay", female lectotype (+ one female paralectotype designated by Papp in 1969, see Shenefelt 1978 l.c.) in Magyar Természettudományi Múzeum, Budapest; examined. – Szépligeti 1906: 590 (in key). Shenefelt 1978: 1523 (as *Bracon paraguayensis*, literature up to 1906). Quicke 1991: 172 (as *Cyclaulax paraguayensis* comb. n., type depository).

*Type designation of Bracon paraguayensis.*—Designation of the female lectotype and one female paralectotype: (first label, my manuscript) "Paraguay / South America" (reverse label of the lectotype) "Paraguay" (with Szépligeti's manuscript); second label is the lectotype and paralectotype cards, respectively, third label is with the inventory numbers 1538 (lectotype) and paralectotype (1539) (second and third labels were attached by me); fourth label is with the actual name *Cyclaulax paraguayensis* (Szépligeti) given by Quicke in 1989. – Lectotype is in fairly good condition: (1) pinned by the mesosoma; (2) both flagelli deficient distally; (3) tarsomeres 3–5 of left middle leg missing; (4) left pair of wings longitudo-distally somewhat creased. – Paralectotype is in poor condition: (1) pinned by the mesosoma; (2) both flagelli deficient distally; (3) metasoma





Figs 77–87. *Cyclaulax paraguayensis* (Szépligeti), female lectotype: 77 = scape in outer-lateral view, 78 = scape in inner-lateral view, 79 = head in dorsal view, 80 = head in lateral view, 81 = tarsus of first leg, 82 = hind femur, 83 = pterostigma and vein *r* of fore wing, 84 = first discal cell of fore wing, 85 = tergites 1–3; female paralectotype: 86 = head in dorsal view, 87 = pterostigma and vein *r* of fore wing

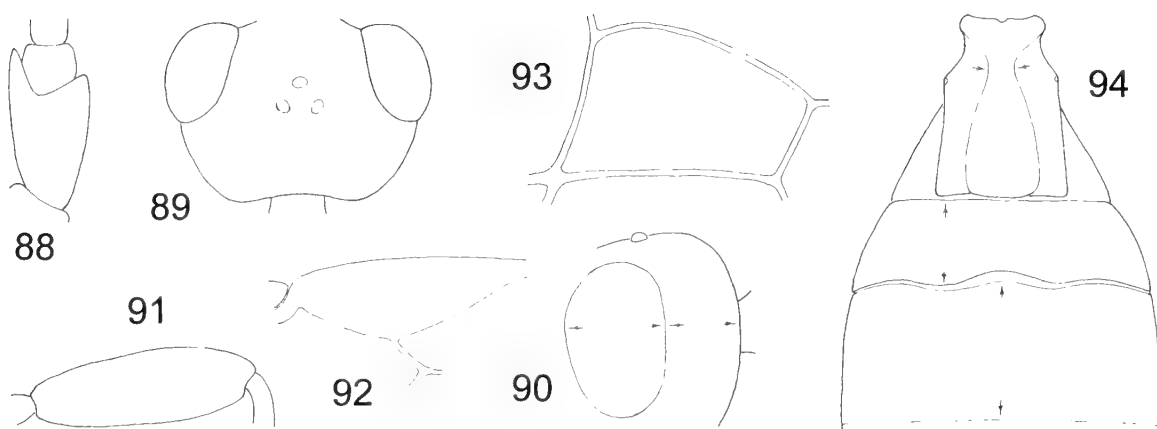
glued on a separate small card; (4) right fore wing missing, left hind wing somewhat creased; (5) left hind leg missing.

**Redescription of the female lectotype of *Bracon paraguayensis*.**—Body 9.5 mm long. Scape in outer-lateral view 1.5 times as long dorsally as broad apically (Fig. 77), in inner-lateral view as in Fig. 78. Both flagelli deficient, right flagellum with 13 and left flagellum with 17 flagellomeres. First flagellomere almost 1.4 times as long as broad and 17th flagellomere cubic. – Head in dorsal view (Fig. 79) less transverse, nearly 1.6 times as broad as long, eye clearly 1.4 times as long as temple, temple less rounded. Eye in lateral view 1.6 times as high as wide and just 1.3 times wider than temple, latter beyond eye evenly broad (Fig. 80).

Mesosoma in lateral view 1.8 times as long as high. Tarsomeres 2–4 of fore leg long, in lateral view third tarsomere twice and fourth tarsomere nearly 1.6 times as

long as broad apically (Fig. 81). Hind femur 3.1 times as long as broad and relatively more broadening distally (Fig. 82). Vein *r* one-fifth shorter than width of pterostigma (Fig. 83). First discal cell fairly high, *1-M* 1.66 times longer than *m-cu*, *1-SR+M* twice longer than *1-M*, *1-M* just bent (Fig. 84). – First tergite almost 1.2 times as long as broad behind, scutum wide; third tergite just 1.5 times as long medially as long second tergite laterally; suture between them trisinate (Fig. 85). Ovipositor sheath as long as hind tibia + tarsomeres 1–2 combined.

Scape black, flagellum brownish black. Ground colour of head and mesosoma black with reddish pattern: upper margin of eye, run of notaulix + hind field and lateral margin of mesoscutum, scutellum medially, metanotum and propodeum. Tegula reddish. Tergites reddish yellow, last two tergites dark brown. Legs tricoloured. Fore leg yellow, coxa brown; mid-



Figs 88–94. *Cyclaulax sicuaniensis* (Szépligeti): 88 = scape in outer-lateral view, 89 = head in dorsal view, 90 = head in lateral view, 91 = hind femur, 92 = pterostigma and vein *r* of fore wing, 93 = first discal cell of fore wing, 94 = tergites 1–3

dle leg: coxa blackish brown, trochanters + femur basally + tibia apically brownish, otherwise leg yellow; hind leg: coxa and trochanters black, femur blackish with very weak reddish tint distally, tibia proximo-distally light brown to dark brown, tarsomeres brown to dark brown, basally and apically reddish to rusty. Wings light brown fumous, pterostigma yellow, veins brown to light brown.

*Redescription of the female paralectotype of Bracon paraguayensis.*—Similar to the female lectotype. Body 9 mm long. Both flagelli deficient: right flagellum with 42 and left flagellum with 28 flagellomeres. First flagellomere hardly 1.4 times as long as broad and 42nd flagellomere transverse, i.e. somewhat broader than long. – Head in dorsal view (Fig. 86) 1.5 times as broad as long, eye 1.4 times as long as temple. Corporal colour similar to that of lectotype except hind leg: coxa black, trochanters + femur + tibia apically dark brown, otherwise leg yellow, tarsi apically brownish.

Deviating features of 13 females (from the locality Paraguay: Hohenau; 12 females in Museum Budapest, 1 female in Museum Leiden). – Similar to the female lectotype and paralectotype. Body 6–9 mm long (6: 1 ♀, 7: 2 ♀♀, 7.5: 3 ♀♀, 8: 4 ♀♀, 8.5: 2 ♀♀, 9: 1 ♀). Antenna (4 ♀♀) about as long as (2 ♀♀) or somewhat longer than body (2 ♀♀) and

with 41, 43 and 47 antennomeres. Flagelli of further (i.e. 10 ♀♀) specimens either deficient or missing. Penultimate flagellomere subcubic, i.e. a bit longer than broad. Head in dorsal view 1.5–1.58 times as broad as long, eye 1.4–1.5 times as long as temple. Hind femur 3.1–3.3 times as long as broad distally. Vein *r* of fore wing as long as width of pterostigma (1 ♀, Fig. 87) or more or less shorter (Fig. 83). First tergite as long as broad behind (2 ♀♀).

Male and host unknown.

*Distribution.*—Paraguay.

*Taxonomic position.*—On the one hand, *C. paraguayensis* appears to be nearest to *C. lunatus* (Szépligeti) on the basis of their broad first tergites, and to *C. flexuosus* (Szépligeti) + *C. sicuaniensis* (Szépligeti) in view of their subcubic heads, on the other. Their separation is presented in key-couplets 4(5) – 5(4) and 13(18) – 17(16).

### *Cyclaulax sicuaniensis* (Szépligeti) (Figs 88–94)

*Bracon sicuaniensis* Szépligeti, 1904: 185 ♀, type locality: "Peru: Sicuani", female holotype (designated by Papp in 1969) in Magyar Természettudományi Múzeum, Budapest; examined. – Szépligeti 1906: 591 (in key). Shenefelt 1978: 1538 (as *Bracon sicuaniensis*, literature up to 1906). Quicke 1991: 173 (as *Cyclaulax sicuaniensis* comb. n., type depository).

*Designation of the female holotype of Bracon sicuaniensis*.—(first label, my hand-script) “Peru / Sicuani”, (reverse label with Szépligeti’s handscript) “Sicuani”; second label is the holotype card and the third label is with the inventory number 1550 (labels 1–3 were attached by me); fourth label is with the actual name *Cyclaulax sicuaniensis* (Szépligeti) given by Quicke in 1989. – Holotype is in fairly poor condition: (1) micropinned by mesosoma, pin covered with copper vitriol crystals; (2) missing: right antenna, left flagellum; (3) wings more or less creased; (4) legs less visible owing to the mounting (specimen on the micropin very near to the polyporus stage).

*Redescription of the female holotype of Bracon sicuaniensis*.—Body 6 mm long. Scape in outer-lateral view 1.65 times as long dorsally as broad apically (Fig. 88). – Head in dorsal view (Fig. 89) less transverse, 1.5 times as broad as long, eye 1.35 times as long as temple, temple clearly narrowing. Eye in lateral view 1.5 times as high as wide and 1.2 times wider than temple, temple beyond eye slightly narrowing ventrally (Fig. 90, see arrows).

Mesosoma in lateral view almost twice as long as high. Hind femur less broadening distally, 2.9 times as long as broad

distally (Fig. 91). Fore wing: vein *r* short, half as long as width of pterostigma (Fig. 92); first discal cell less high, 1–*M* 1.5 times as long as *m*–*cu*, 1–*M* weakly bent (Fig. 93). – First tergite 1.33 times as long as broad behind, its scutum less narrowing anteriorly; third tergite nearly 1.6 times longer medially than second tergite laterally; suture between them medially less sinuate (Fig. 94, see arrows). Ovipositor sheath shorter than hind tibia + tarsus combined.

Scape blackish. Head and mesosoma black, upper margin of pronotum and propodeum entirely with faint rusty tint. Metasoma reddish yellow, apically blackish. Legs black to brown, coxa + trochanters + femur of fore leg and femur of middle leg yellow. Wings dark brown fumous, pterostigma brown, veins dark to light brown.

Male and host unknown.

*Distribution*.—Peru.

*Taxonomic position*.—*C. sicuaniensis* is nearest to *C. flexuosus* (Szépligeti) in view of their cubic heads, suture between tergites 2–3 medially less deeply sinuate and first tergite clearly longer than broad behind; for their distinction see key-couplets 15(14) – 17(16).

KEY TO THE CYCLAULAX SPECIES DESCRIBED BY SZÉPLIGETI AND C. GRANDICEPS OF THE NEOTROPICAL REGION

(KEY BASED MAINLY ON THE FEMALES)

- 1 (6) First tergite broad, i.e. at least as long as broad behind (Figs 66, 85) or broader behind than long (Fig. 49). Suture between tergites 2–3 clearly trisinuate (Figs 49, 66, 85). .
- 2 (3) First tergite broader behind than long (Fig. 49). Inner spur of middle tibia slightly longer than half basitarsus (Fig. 43). Ground colour of body reddish yellow, head black. Eye in dorsal view almost 1.4 times as long as temple (Fig. 38). Vein *r* issuing proximally from middle of pterostigma (Fig. 48). Face entirely black. ♀: 12 mm. – Guiana . . . . . *C. grandiceps* Cameron, 1911
- 3 (2) First tergite at most as long as broad behind (Figs 66, 85). Inner spur of middle tibia at most as long as half basitarsus as usually (Fig. 63). Ground colour of body testaceous to reddish, reddish yellow with more or less black pattern. . . . .
- 4 (5) Eye in dorsal view 1.7 times as long as temple (Fig. 61). Vein *r* somewhat longer than width of pterostigma and issuing from its middle (Fig. 65). Pterostigma blackish brown. First tergite as long as broad behind (Fig. 66). Scape in lateral view 1.6 times as long ventrally as broad apically (Fig. 60). Head in dorsal view 1.55–1.6 times as

- broad as long (Fig. 61). Ground colour of body testaceous to reddish yellow with black to blackish pattern on tergi. Head black. Median granulose field of face with luniform yellow macula. ♀: 8–10 mm. – Peru . . . . . *C. lunatus* (Szépligeti, 1906)
- 5 (4) Eye in dorsal view 1.5–1.4 times as long as temple (Fig. 79). Vein *r* shorter than width of pterostigma and issuing from its middle (Fig. 83), exceptionally *r* as long as width of pterostigma. Pterostigma yellow. First tergite somewhat longer than broad behind (Fig. 85) and less usually as long as broad behind. Further details see couplet 14(15) . . . . . *C. paraguayensis* (Szépligeti, 1914)
- 6 (1) First tergite less broad, i.e. more or less longer than broad behind; suture between tergites 2–3 less variably trisinate (Figs 7, 14, 23, 33, 57, 75, 94). . . . .
- 7 (8) Head in dorsal view transverse, almost 1.9 times as broad as long, temple constricted, eye clearly twice as long as temple (Fig. 10). Hind femur 3.5–3.6 times as long as broad distally (Figs 12, 15). First tergite 1.55–1.6 times as long as broad behind, its lateral part narrow, third tergite about one-fifth longer than second tergite (Fig. 14). Tergites black; labrum + clypeus + cheek yellow or reddish yellow. ♀: 6.5–7 mm. – Peru . . . . . *C. binotatus* (Szépligeti, 1904)
- 8 (7) Head in dorsal view less transverse, 1.5–1.7 times as broad as long, temple rounded to receded (Figs 27, 52, 69, 79). . . . .
- 9 (12) Tarsomeres 2–4 of fore leg in lateral view short, third tarsomere nearly 1.4 times as long as high and fourth tarsomere cubic (Fig. 55, 72), fore tarsus yellow. . . . .
- 10 (11) Third tergite 1.5–1.4 times as long as second tergite; median sinuation of suture between tergites 2–3 deep (Fig. 57). Scutum of first tergite less narrow, i.e. lateral part of tergite less wide (Fig. 57). Hind femur 3.5–3.6 times as long as broad (Fig. 54). Ovipositor sheath as long as body. Only fore tarsus yellow. ♀: 7.5–8 mm. – Bolivia, Peru . . . . . *C. linurus* (Szépligeti, 1906)
- 11 (10) Third tergite nearly twice as long as second tergite; median sinuation of suture between tergites 2–3 less deep (Fig. 75). Scutum of first tergite narrow, i.e. lateral part of tergite wide (Fig. 75). Hind femur 2.9 times as long as broad (Fig. 73). Ovipositor sheath as long as metasoma. Fore and middle tarsi yellow. ♀: 9 mm. – Bolivia . . . . . *C. mesonurus* (Szépligeti, 1906)
- 12(9) Tarsomeres 2–4 of fore leg in lateral view long, third tarsomere twice and fourth tarsomere 1.3–1.5 times as long as high (Figs 4, 81), tarsus black. . . . .
- 13 (18) Head in dorsal view subcubic, 1.5–1.55 times as broad as long (Figs 27, 79, 86, 89). Scape in lateral view 1.5 times as long dorsally as broad apically (Figs 26, 77–78, 88).
- 14 (15) First tergite slightly (1.1–1.2 times) longer than (Fig. 85) or at most (and rather rarely) as long as broad behind. Hind femur more broadening distally, 3.1 times as long as broad distally (Fig. 82). Suture medially (between tergites 2–3) more sinuate (Fig. 85). Vein *r* as long as (Fig. 87) or, as usually, slightly shorter (Fig. 83) than width of pterostigma. Pterostigma and fore leg (except brownish coxa) yellow. ♀: (6–)8–9.5 mm. – Paraguay . . . . . *C. paraguayensis* (Szépligeti, 1904)
- 15 (14) First tergite clearly (1.3–1.4 times) longer than broad behind (Figs 33, 94). Hind femur less broadening distally (Figs 30, 91). Suture medially (between tergites 2–3) less sinuate (Figs 33, 94). Vein *r* shorter than width of pterostigma (Figs 31, 92). Pterostigma dark to blackish brown; fore leg either brown or yellow. . . . .
- 16 (17) Temple in dorsal view moderately rounded (Fig. 27). Scutum of first tergite more narrowing anteriorly (Fig. 33, see arrows). Vein *r* clearly longer than half width of pterostigma (Fig. 31). Fore coxa + femur and middle femur rusty brown. ♂: 6–7.5 mm. – Venezuela . . . . . *C. flexuosus* (Szépligeti, 1902)
- 17(16) Temple in dorsal view clearly narrowing (Fig. 89). Scutum of first tergite less narrowing anteriorly (Fig. 94, see arrows). Vein *r* half as long as width of pterostigma (Fig. 92). Fore coxa + femur and middle femur yellow. ♀: 6 mm. – Peru . . . . . *C. sicuaniensis* (Szépligeti, 1904)
- 18 (13) Head in dorsal view transverse, 1.6–1.7 times as broad as long (Figs 1, 19). Scape in lateral view 1.7 times to twice as long dorsally as apically (Figs 18, 60). . . . .

- 19 (20) Second tergite less short, third tergite nearly 1.4 times as long as second tergite; first tergite 1.2 times as long as broad behind, scutum of tergite wide (Fig. 23, see arrows). First discal cell less high, 1-M straight veins relatively thin as usually (Fig. 22). Hind femur 3.6–3.3 times as long as broad medially (Figs 21, 25). Fore coxa yellowish. ♀: 8–9 mm. – Peru . . . . . *C. enotatus* (Szépligeti, 1904)
- 20(19) Second tergite short, third tergite 1.6 times as long as second tergite; first tergite 1.4 times as long as broad behind, scutum of tergite less wide (Fig. 7, see arrows). First discal cell high, 1-M bent, veins relatively thick (Fig. 6). Hind femur 2.9–3.1 times as long as broad medially (Figs 3, 8). Fore coxa blackish brown. ♀: 8–9 mm. – Peru . . . . . *C. atriceps* (Szépligeti, 1904)

SPECIES OF THE GENUS  
CYCLAULAX CAMERON, 1911

- atriceps* (Szépligeti, 1904) (*Bracon*) – Peru
- binotatus* (Szépligeti, 1904) (*Bracon*) – Peru
- crassitarsis* (Brues, 1912) (*Bracon*) – Brazil
- enotatus* (Szépligeti, 1904) (*Bracon*) – Peru
- flexuosus* (Szépligeti, 1904) (*Bracon*) – Venezuela
- grandiceps* Cameron, 1911 – Guiana
- linurus* (Szépligeti, 1906) (*Bracon*) – Bolivia, Peru
- lunatus* (Szépligeti, 1906) (*Bracon*) – Peru
- mesonurus* (Szépligeti, 1906) (*Bracon*) – Bolivia, Peru
- paraguayensis* (Szépligeti, 1904) (*Bracon*) – Paraguay
- sicuanimensis* (Szépligeti, 1904) (*Bracon*) – Peru

Remark.—*Cyclaulax crassitarsis* (Brues) remains unknown to me, hence not included in the present article. The species was assigned to *Cyclaulax* by Quicke (1989: 119).

ACKNOWLEDGEMENTS

Mrs S. Ryder (The Natural History Museum, London) was kind enough to place at my disposal for examination the “Type” specimen of *Cyclaulax grandiceps* Cameron. My sincere gratitude should go to her cooperation in this respect. The examination of the generic type *C. grandiceps* essentially promoted my knowledge of the generic features of *Cyclaulax*

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## Three New Species of Cenocoeliinae (Hymenoptera: Braconidae) with Novel Morphological Characteristics and Habitat Records

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**Abstract.**—The purpose of this paper is to introduce three new Neotropical species of cenocoeliine wasps that expand the morphological and biological boundaries of the subfamily. These three species share a complex of morphological characters that distinguish them from other known species of *Capitonius*, and because of this we propose these species form a distinctive and monophyletic species group. Unlike other members of the subfamily, the new species are dorsoventrally flattened and represent some of the smallest recorded cenocoeliines. The following species are described; *Capitonius subcrusta* Pitz and Sharkey n. sp. from Mexico, *C. vegrandis* Pitz and Sharkey n. sp. from Costa Rica, and *C. tenuiflagellum* Pitz and Sharkey n. sp. from Colombia.

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The subfamily Cenocoeliinae is relatively small with approximately 70 described species (Achterberg 1997, Braet and van Achterberg 2001, Yu et al. 2005). The few cenocoeliines with known biologies are koinobiont endoparasitoids of mostly wood-feeding coleopteran larvae, mainly in the families Cerambycidae and Curculionidae (Scolytinae) but with some host records of Buprestidae and non-scolytine Curculionidae (Saffer 1982, Shaw and Huddleston 1991). Cenocoeliines are known to parasitize hosts that utilize a variety of woody substrates, ranging from tree trunks (personal observation) to smaller branches and twigs (Shaw 1999), with scattered records from a variety of other plant material such as herbaceous stems, fruits, and nuts (Saffer 1982). Although cenocoeliines are cosmopolitan (van Achterberg 1997, Pitz and Sharkey 2005), they are most diverse in the neotropics. The subfamily has been largely overlooked in the past, leaving many new species to be described (Achterberg 1997, Ent and Shaw 1998).

Here, we describe three new species of Cenocoeliinae collected in Mexico, Costa Rica, and Colombia. These new species differ from other cenocoeliines in several ways. The mesosoma is dorsoventrally flattened (Fig. 1). The metasoma is inserted only slightly above the hind coxae (Fig. 1). The hind coxal grooves, which are ovipositor guides, are located along the anterior margin of the medial face of the hind coxae (Fig. 2d). The antennal scrobe is truncated and shallow, leaving the median ocellus outside the antennal scrobe and level with the lateral ocelli (Fig. 3a–c). The scape is swollen in the apical half (Fig. 4a). Females have short, thick antennae; the flagellomeres are about as wide as long, most having only a single row of longitudinal placodes that are nearly as long as a flagellomere (Fig 4b). Males (Fig. 5b) have normal antennae with flagellomeres that are about twice as long as wide, each with multiple rows of placodes that range from one third to one half the length of a flagellomere. Finally, these wasps are some of the smallest members of the

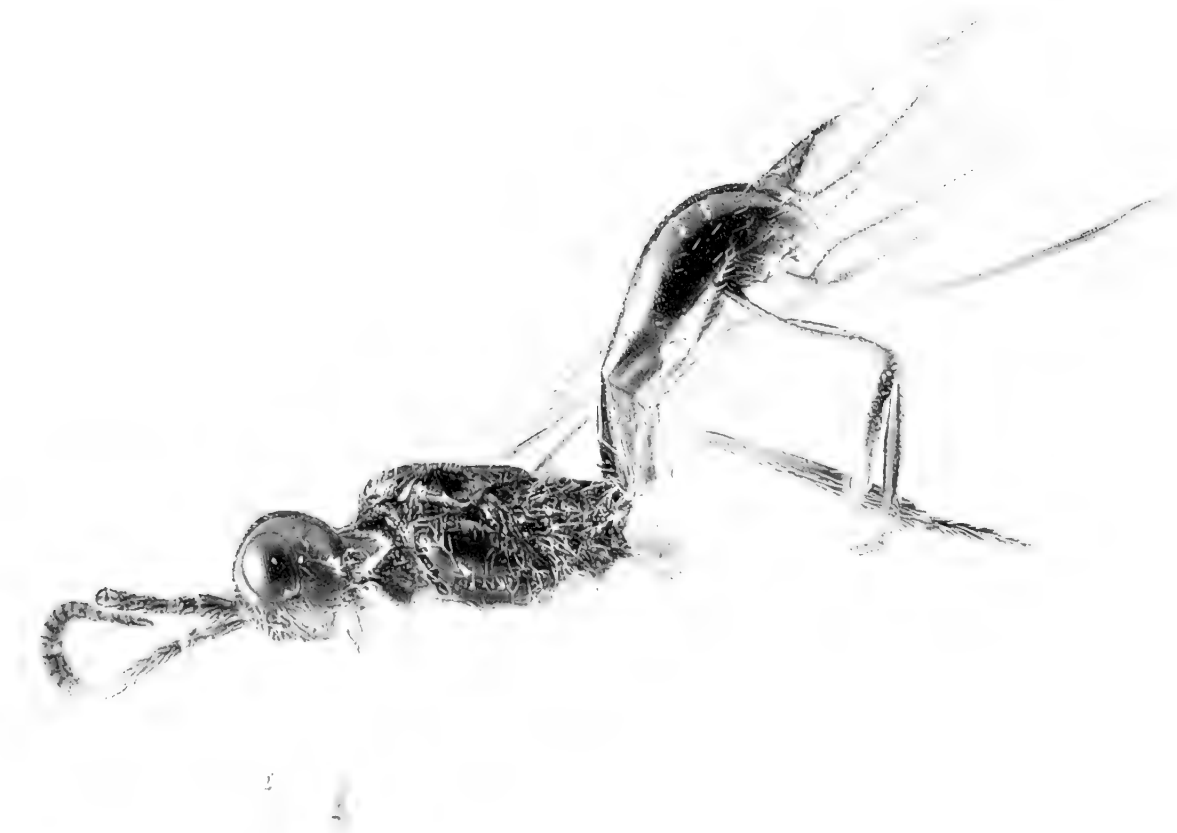


Fig. 1. *Capitonius vegrandis*, holotype female.

subfamily Cenocoeliinae, with a maximum length of 3.28 mm. All of these characters are putative synapomorphies of the three newly described species. One of these remarkable species has lost the r-m cross-vein of the forewing (Fig. 3g), the first report of this characteristic for the subfamily.

#### DISCUSSION

Collection labels of the Mexican specimens state that they were found under the bark of a tree and we suggest that the dorsoventrally flattened body is an adaptation for this habitat. Unrelated species in the genus *Chartobracon* (Braconinae) have members that are also dorsoventrally flattened (van Achterberg 1983). The type species, *Chartobracon huggerti* Achterberg, was reared from cocoons collected from cerambycid tunnels under the bark of

spruce trees (van Achterberg 1983), and other adult specimens were collected under the bark of trees (Quicke and Sharkey 1989). Species of *Chartobracon* range between 2.7–2.9 mm in body length, (van Achterberg 1983, Quicke and Sharkey 1989). These observations are consistent with the hypothesis presented here, i.e., the small flattened bodies of braconids attacking xylophagous beetles are adaptations to facilitate searching for hosts under bark.

Both the newly described species of *Capitonius* and species of *Chartobracon* have short ovipositors, ranging between 1.96–2.24 mm for the new species of *Capitonius*, and 1.2 mm for *Chartobracon* (Quicke and Sharkey 1989), such that they would not be able to penetrate far into any substrate. This suggests these species may oviposit directly into the host larvae. This is in contrast to other dorsoventrally flattened

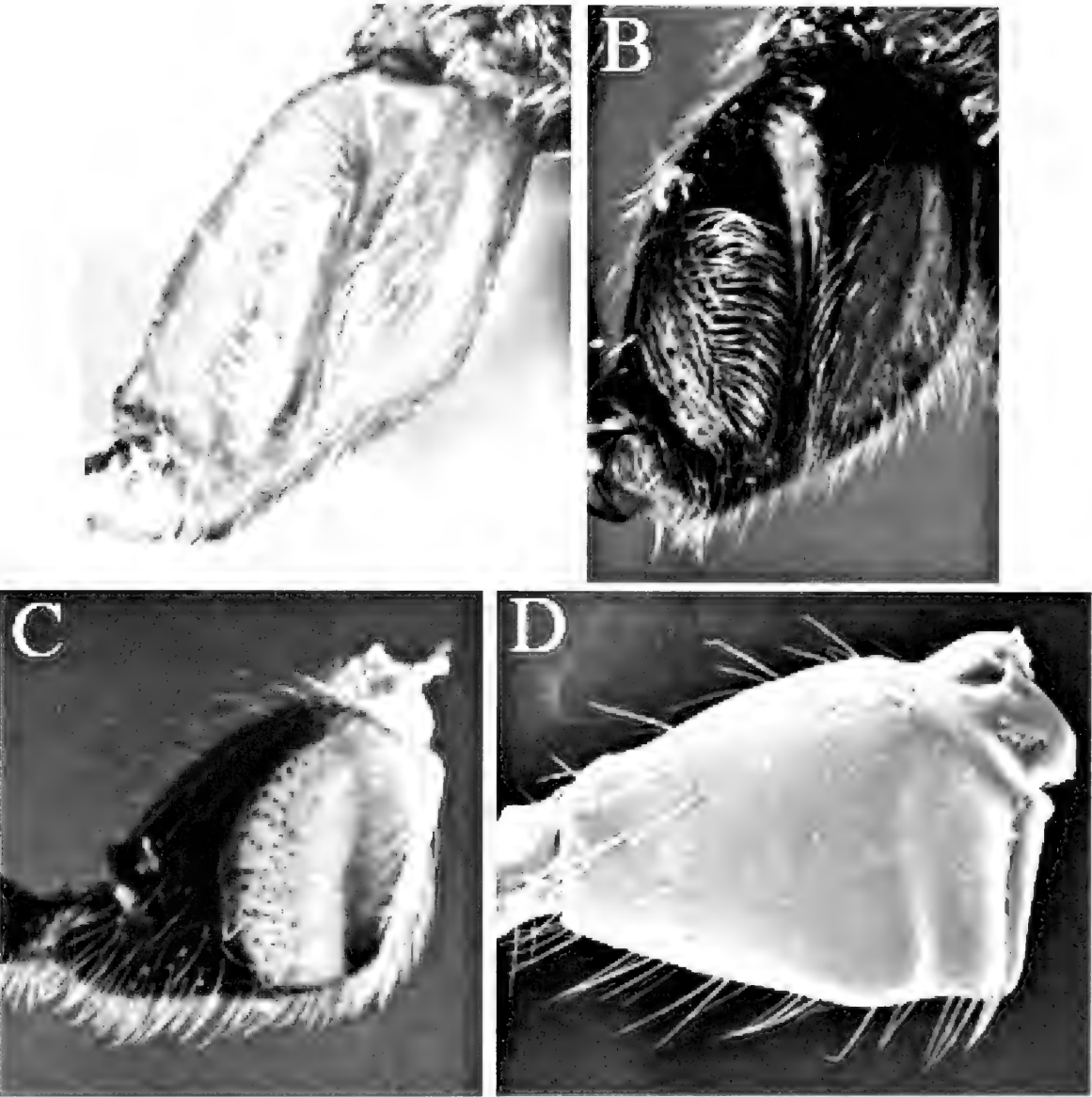


Fig. 2. Hind coxal grooves of female cenocoeliines: a, *Foenomorpha filicornis*; b, undescribed species of *Cenocoelius* from Arizona, USA; c, *Capitonius chontalensis*; d, *Capitonius subcrusta*.

species, such as those in the genus *Atanycolus* that are known to use their ovipositors to penetrate the host's substrate from the outside; these wasps are larger (over 5 mm) with longer ovipositors that allow them to penetrate into a substrate far enough to reach host larvae.

Some cenocoeliines, such as *Foenomorpha filicornis* (Cameron), have a groove on the medial surface of the hind coxa that is situated along the longitudinal axis. This directs the ovipositor posteroventrally dur-

ing oviposition (Fig. 2a). Other species, such as *Capitonius chontalensis* (Cameron), have a groove that is situated along the vertical axis of the coxa, between the midline and anterior margin that directs the ovipositor ventrally during oviposition (Fig. 2c). There are also species of Cenocoeliinae, such as an undescribed species of *Cenocoelius* from Arizona, which have an intermediate position of the hind coxal grooves angled somewhere between the previously discussed orientations (Fig. 2b).

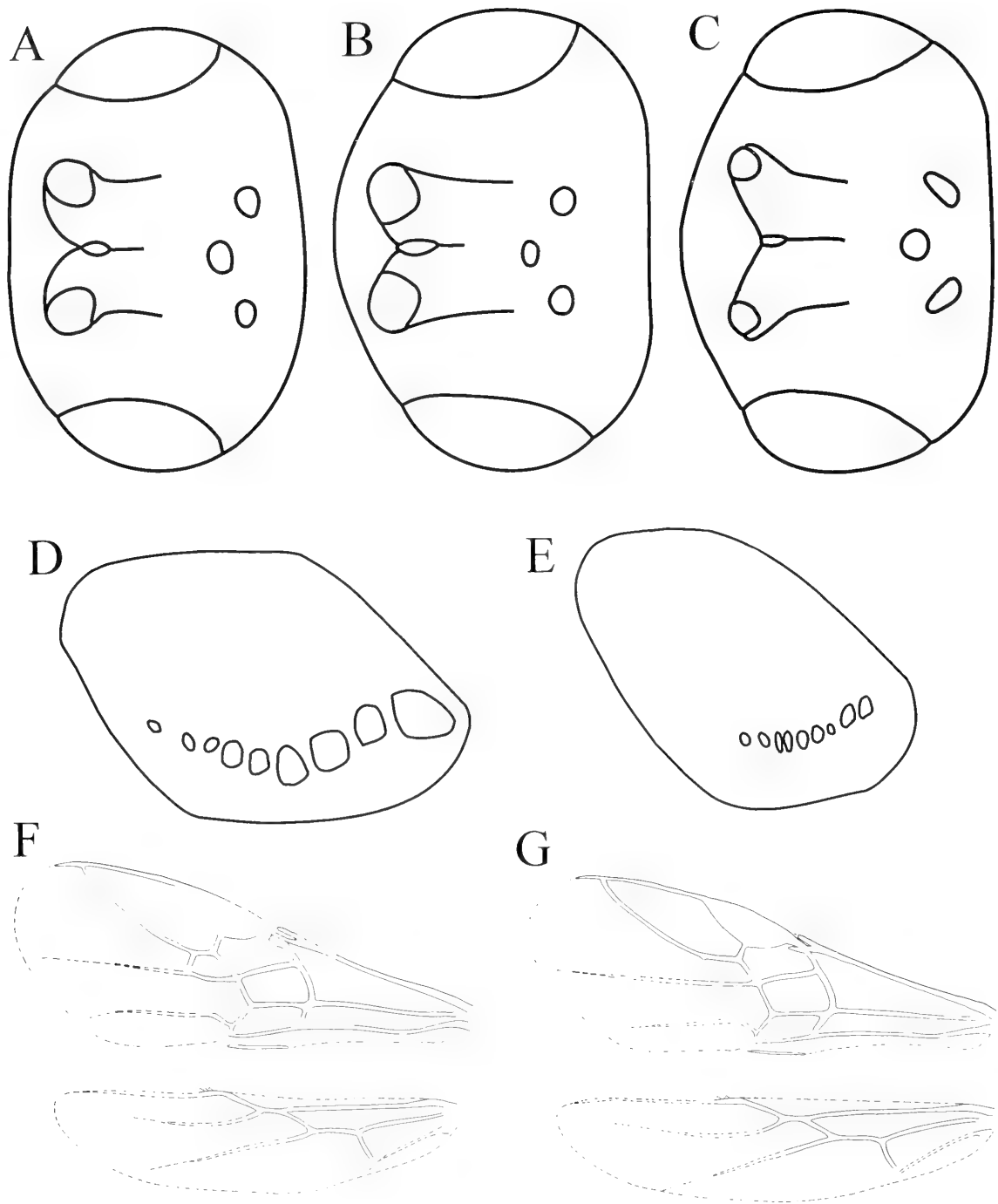


Fig. 3. Illustrations of new species of *Capitonius*: a, *C. subcrusta* dorsal head; b, *C. tenuiflagellum* dorsal head; c, *C. vegrandis* dorsal head; d, *C. tenuiflagellum* lateral mesosoma illustrating sternaulus; e, *C. subcrusta* lateral mesosoma illustrating sternaulus; f, *C. subcrusta* wings; g, *C. vegrandis* wings.

The ovipositor guides on the hind coxae of the newly proposed species are located along the anterior margin of the hind coxae and indicate that the ovipositor is directed anteroventrally during oviposition (Fig. 2d).

In most cenocoeliines, the ratio of the ovipositor to body length is proportional to the angle of the ovipositor guide, such that the longest ovipositors are found in species with guides that are almost parallel to the long axis of the coxae, and shorter ovipo-

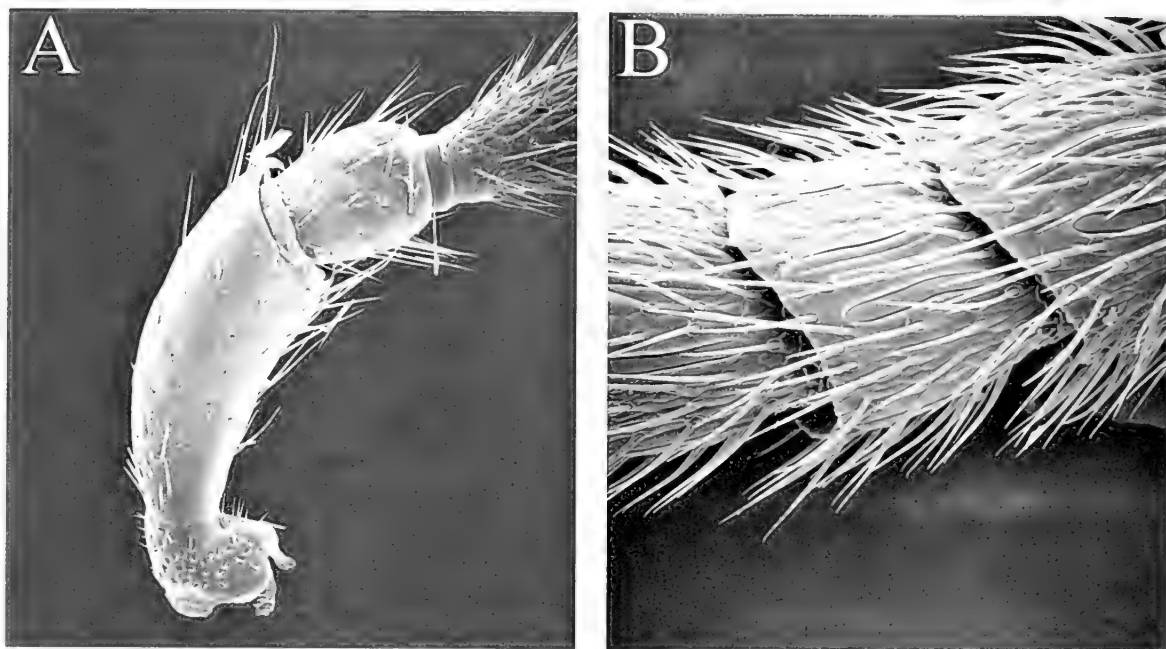


Fig. 4. *Capitonius subcrusta*: a, scape, paratype female; b, flagellomeres, paratype female.

sitors are found in species with grooves that direct the ovipositor ventrally. Examining a randomly chosen representative from the species discussed above, we found *F. filicornis* had an ovipositor: body length ratio of 1.57, the undescribed species of *Cenocoelius* from Arizona had a ratio of 1.43, and *C. chontalensis* had a ratio of 1.29, demonstrating that species with grooves that run closer to parallel to the midlength of the hind coxae tend to have longer ovipositors in relation to their body length. The newly described species have some of the shortest ovipositor: body ratios found in *Cenocoeliinae*, with ratios of 0.66, 0.73, and 0.67 for *C. tenuiflagellum*, *C. subcrusta*, and *C. vegrans* respectively. They also have the most anteriorly located ovipositor guides of any known member of the subfamily.

Based on the microhabitat in which the Mexican specimens were collected, the orientation of the ovipositor guides, the small body size, and the short ovipositor length, we hypothesize members of the new species-group do not drill or probe into the woody substrate from the outside

of the tree, as is typical of other members of the subfamily, but crawl under the bark and directly parasitize hosts. Morphological features of the antennal scrobe also corroborate this hypothesis. The three species described here have truncated and shallow antennal scrobes, whereas all other members of the *Cenocoeliinae* have deep antennal scrobes that extend to the lateral ocelli. The antennal scrobe is a modification found in many hymenopterans that emerge from tunnels in wood. While emerging from the host substrate, the antennae are folded back and fit into the scrobe, thereby protecting them as the wasps emerge. All three new species have very shallow and truncated antennal scrobes suggesting that they have no need to protect the antennae.

Generic limits are not yet well established in the *Cenocoeliinae*, making placement of these species problematic. In the most recent treatment of the group, van Achterberg's (1994) generic concepts are based on suites of characters, and lack a phylogenetic framework. His keys and diagnoses must be used to under-



Fig. 5. *Capitonius tenuiflagellum*: a, lateral habitus , holotype female; b, lateral habitus, paratype male.

stand generic limits. Recent molecular analyses (Pitz in prep) provide a clearer understanding of relationships within Cenocoeliinae, though molecular data were not collected from these three species.

## MATERIALS AND METHODS

Generic placement of the three new species is based on the results of phylogenetic analyses of cenocoeliine genera (Pitz in prep.). We tentatively assign these species to the genus *Capitonius* primarily based on the ratios of the hind wing veins M+CU to 1M; no molecular data are available for the newly described species, but their hind wing vein ratios are within the range found for other species of *Capitonius*. The specimens were compared to original descriptions and determined specimens of *Capitonius* to establish that they represent new species.

Morphological terminology used follows that of Sharkey and Wharton (1997). All photographs were taken using a JVC KY-F75 3CCD digital camera attached to a Leica MZ-16 stereoscope and were prepared using and measurements made with software in an Auto-Montage<sup>®</sup> imaging system. Scanning Electron Micrographs were produced using a Hitachi S-800 Field Emission Scanning Electron Microscope.

### *Capitonius subcrusta* Species Group

**Description.—Female. Length:** 2.68–3.40 mm. **Head:** Antenna shorter than forewing, with 22 flagellomeres [on intact specimens], scape swollen apically (Fig. 4a), flagellomeres with single row of longitudinal placodes which are almost the length of the flagellomere (Fig. 4b); antennal scrobe greatly reduced, ending immediately anterior to median ocellus, carina along antennal scrobe ending before lateral ocellus (Fig. 3a–c); frons slightly convex laterally, medial lamella of antennal scrobe short; vertex smooth, with sparse, weak punctures and sparse setae laterally; area

posterior to lateral ocellus flat to slightly convex; face and clypeus smooth with sparse punctures and setae; clypeus with medioventral tooth, occipital carina smoothly rounded dorsomedially, without a sharp angle. **Mesosoma:** Dorsoventrally compressed (Figs. 1,5,6); pronotum not distinctly protruding anterodorsally, with large triangular pronope, and large triangular sub-pronope; propleuron without transverse carina; mesopleuron smooth with sparse setae; mesoscutum smooth with sparse setae, notauli narrow, composed of moderately sized rectangular fovea, nearly united immediately anterior to transscutal articulation; transscutal articulation not impressed as a groove, present as a line near midline only; scutellum without medioposterior depression; metanotum moderately crenulate; metapleuron and propodeum irregularly areolate; hind coxal groove sharply defined, situated along anterior edge of hind coxa (Fig. 2d); forefemur normal, not flanged; rectangular space between hind coxae and metasomal insertion (metasomal pseudosternite) delineated by four strong carinae; transverse groove of metapleuron at level of episternal scrobe; tarsal claws simple. **Wing:** Vein 1-M slightly curved (Fig. 3f–g); crossvein 1r-m present or absent. **Metasoma:** Second median tergite smooth; third median tergite smooth and without acute lateral margin.

**Male** (Fig. 5b) – as in female except for primary sexual characters and male antenna longer than forewing, with 24 flagellomeres, scape not swollen apically, flagellomeres with two to three rows of longitudinal placodes.

**Diagnosis.**—These species are the only known members of *Capitonius* that have the following suite of characters: body dorsoventrally flattened, antennal scrobe reduced, female with short and thick flagellomeres, female with hind coxal groove situated at extreme anterior margin of coxa. This species group has a larger suite of hypothesized synapomorphies than *Ca-*





Fig. 6. Lateral habitus, holotype female, *Capitonius subcrusta*.

*pitonius* itself, providing a high level of support for the proposed monophyly of *C. subcrusta*, *C. tenuiflagellum*, and *C. vegrandis*.

*Distribution*.—Southern Nearctic to northern Neotropical (Mexico to Colombia). Containing only three known species.

KEY TO SPECIES OF THE SUBCRUSTA GROUP

- 1. Second cubital cell present (Fig. 3f) ..... 2
- Second cubital cell absent (Fig. 3g) ..... *Capitonius vegrandis* Pitz and Sharkey n. sp.
- 2. Sternaulus complete, composed mostly of large, subovoid fovea (fig. 3d); carina bordering antennal scrobe nearly complete, ending three quarters of the way to lateral ocellus from antennal insertion (Fig. 3b). ..... *Capitonius tenuiflagellum* Pitz and Sharkey n. sp.
- Sternaulus present only over posterior three-quarters of metapleuron, composed of small to moderate sized ovoid fovea (Fig. 3e); carina bordering antennal scrobe truncated, ending approximately halfway between antennal insertion and lateral ocellus (Fig. 3a) ..... *Capitonius subcrusta* Pitz and Sharkey n. sp.

***Capitonius subcrusta* Pitz and Sharkey  
n. sp.**

*Etymology*.—Latin for under bark; a reference to the microhabitat in which all known specimens were collected

*Description*.—**Holotype Female** (Fig. 6). **Length**: 2.68 mm. **Color**: Body mostly melanic except testaceous (yellowish brown) as follows: ventral margin of malar space and clypeus; mandible basally; fore- and midlegs, hind tibia basally. Wings clear with stigma melanic; ovipositor reddish brown. **Head**: Antenna with 22 flagellomeres; lateral carina bordering antennal scrobe reduced, ending far anterior to lateral ocellus (Fig. 3a); median lamella of antennal scrobe wide and slightly flat-tented anteriorly becoming acute posteriorly. **Mesosoma**: Pronotum with three large fovea extending from sub-pronope along posterior margin, lateral margin weakly rugose, otherwise pronotum smooth; scutellar sulcus with four fovea; propleuron smooth with moderately dense setae; sternaulus incomplete, only occupying posterior three-quarters of mesopleuron, composed of single row of fovea (Fig. 3e); space between hind coxae and metasomal insertion weakly rugose between carinae. **Wings**: Second submarginal cell present (Fig. 3f). **Metasoma**: First median tergite smooth; length 1.03 times its apical width; length of ovipositor:length of forewing ratio 0.71.

*Biology*.—Unknown. Specimens found under bark.

*Male*.—As in female except for primary sexual characters and male antenna longer than forewing, with 25 flagellomeres, scape not swollen apically, flagellomeres with two to three rows of longitudinal placodes.

*Material Examined*.—Holotype female: MEXICO: Tam[auli]p[a]s., Mun.[icipio] Gomez Far-  
ias, Altas Cimas, 1000 m., 8-9.III.1986, P. Kovarik, K. Haack, under bark. Deposited in Texas A&M University Collection.

Paratype male: MEXICO: MEXICO: Chipas, Lagunas de Montebello Nat[ional] Park, 11.VIII.1990 el[elevation] 5000' [1524m], J.B. Woolley. Deposited in Texas A&M University Collection.

***Capitonius tenuiflagellum* Pitz and  
Sharkey n. sp.**

*Etymology*.—Latin for small whip; a reference to the short antennae of the female.

*Description*.—**Holotype Female** (Fig. 5a). **Length**: 3.40 mm. **Color**: Body mostly melanic except testaceous (yellowish brown) as follows: head below level of antennal insertion; mandible basally; all legs except dorsal face of all tibiae, fore and mid basitarsi, hind tarsus, hind tibia basally. Wings clear with stigma melanic; ovipositor reddish brown. **Head**: [Antenna broken, 16 flagellomeres remaining on right, 11 on left]; lateral carina bordering antennal scrobe nearly complete, ending immediately anterior to lateral ocellus (Fig. 3b); median lamella of antennal scrobe acute over entire length. **Mesosoma**: Pronotum with four large fovea extending from sub-pronope along posterior margin, lateral margins weakly rugose, otherwise pronotum smooth; scutellar sulcus with four fovea; propleuron smooth with moderately dense setae; sternaulus complete, composed of single row of fovea (Fig. 3d); space between hind coxae and metasomal insertion with area between carinae rugosofoveate. **Wings**: Second submarginal cell present. **Metasoma**: First median tergite with two strong carinae basally, 1.40 times its apical width; length of ovipositor:length of forewing ratio 0.77.

*Biology*.—Unknown.

*Male*.—(Fig. 5b) – As in female except for primary sexual characters and male antenna longer than forewing, with 24 flagellomeres, scape not swollen apically, flagellomeres with two to three rows of longitudinal placodes.

*Material Examined*.—Holotype female: COLOMBIA, Amazonas, PNN Amacayacu, Mata-mata, 3 23'S 70 06'W, 150m, Apr [il] 02-11/

2000, M.101, A. Parente Leg., [Amazonian rainforest]. Deposited in the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia.

Paratype male: COLOMBIA: Amazonas, PNN Amacayacu, Lorena, 3°02.86'S 69°59.7'W. 200 m., red [sweep net], 28.vii.2001, M. Sharkey & D. Campos [Amazonian rainforest]. Deposited in the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia.

Paratype male: Amazonas, PNN Amacayacu, Matamata, 3°23'S 70°06'W, 150m., Mar[ch] 12–19.2000, A. Parente Leg., [Amazonian rainforest]. Deposited in the Hymenoptera Institute Collection, University of Kentucky, Lexington.

*Capitonius vegrandis* Pitz and Sharkey  
n. sp.

*Etymology*.—Latin for tiny or diminutive, in reference to the short body length.

*Description*.—**Holotype Female** (Fig. 1). **Length**: 2.95 mm. **Color**: Body mostly melanic except testaceous (yellowish brown) as follows: malar space; mandible basally, foreleg except apical tarsomere; midleg except apical and basal tarsomeres; wings clear with stigma melanic; ovipositor reddish brown. **Head**: Antenna with 22 flagellomeres, lateral carina bordering antennal scrobe distinctly reduced, ending far anterior to lateral ocellus (Fig 3c); median lamella of antennal scrobe wide and blunt anteriorly, becoming narrow and acute posteriorly. **Mesosoma**: Pronotum with seven large fovea extending from subpronope to posteroventral corner, lateral margin smooth, otherwise pronotum smooth; scutellar sulcus with five fovea; propleuron smooth and bare; sternaulus complete, composed of single row of fovea (Fig 1); space between hind coxae and metasomal insertion (propodeal pseudosternite) weakly rugose between carinae. **Wings**: Second submarginal cell absent (Fig. 3g). **Metasoma**: First median tergite smooth; 1.26 times its apical width; length of ovipositor / length of forewing ratio = 0.61.

*Biology*.—unknown

*Male*.—unknown.

**Material Examined**.—Holotype female: COSTA RICA, Prov.[incia] Punta.[renas], La Casona, R.B., Monteverde, [10° 17' 54.3376" N 84° 47' 33.1719"W], 1520m. Abr [April] 1994. N. Obando, L, N 253250\_449700 #2820. Second label: COSTA RICA INBIO CRI001781333 [with bar code]. Deposited in Instituto Nacional de Biodiversidad, Costa Rica.

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## The Male of *Megachile nivalis* Friese, with an Updated Key to Members of the Subgenus *Megachile* s. str. (Hymenoptera: Megachilidae) in North America

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**Abstract.**—The previously unknown male of *Megachile nivalis* Friese is described. Males of this species are very similar to those of *M. relativa* Cresson and because of geographic overlap of the two species, many male specimens presently identified as *M. relativa* within collections may actually be *M. nivalis*. An identification key and illustrations of mandibles are provided for females and males of the subgenus *Megachile* s. str. of North America. Images of genitalia, selected sterna, the lower genal area, clypeus, and forewings for males of both *M. relativa* and *M. nivalis* are also provided for comparison and to facilitate differentiation of the two species. A tabular summary is also provided for species of *Megachile* in North America that are known from only one sex to encourage the search for possible additional synonyms or hitherto unknown sexes.

**Key words.**—Apoidea, Megachilidae, *Megachile* (*Megachile*), *Megachile nivalis*, male description, North America

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Leafcutter and mason bees of the genus *Megachile* Latreille (Hymenoptera: Megachilidae) are a common and diverse group (Mitchell 1980, O'Toole and Raw 1991, Michener et al. 1994, Baker and Engel 2006) whose members display many morphological and behavioral adaptations (Michener 2000). Currently, 55 extant subgenera are recognized (Baker and Engel 2006), 30 of which are known from the western Hemisphere. In North America, thirteen subgenera are indigenous, but an additional three have been introduced (Michener 2000, Cane 2003). Hurd (in Krombein et al. 1979) listed 134 species of *Megachile* in North America north of Mexico (including the genus *Chalicodoma*); Michener et al. (1994) indicate 139 species. Since the publication of Krombein et al. (1979), at least 111 of the cataloged North American species have undergone changes in subgeneric allocation (Raw 2002), and

Raw (2004) indicates that the 519 described species of *Megachile* in the Western Hemisphere are now allocated to their proper subgenus.

Much is known about the biology of many leafcutter bees due to their importance in crop pollination (Pengelly 1955, Osgood 1974, Ivanochko 1979, Peterson et al. 1992, Free 1993, Richards 1993, Delaplane and Mayer 2000, Raw 2002) and the fact that many species accept trap-nests (Medler 1959, 1964, Fye 1965, Krombein 1967, Frolich and Parker 1983, O'Toole and Raw 1991). Most members of the genus nest above ground in pre-existing cavities or excavate into pithy stems or decomposing wood (Stephen 1956, Ivanochko 1979). Trap-nesting of bees allows detailed study of life-history, nest building, provisioning and egg laying behaviors (Medler 1959, 1964, Klostermeyer and Gerber 1969, Frolich and Parker 1983, Kim 1992), and

incidences of cleptoparasitism (Scott et al. 2000); it also allows one to associate males and females of the same species. However, several North American species within the subgenera *Argyropile*, *Litomegachile*, *Megachiloides* (including *Derotropis* and *Xeromegachile*), and *Xanthosarus* (including *Delomegachile* and *Phaenosarus*) are ground-nesters (Eickwort et al. 1981, Williams et al. 1986, Krombein and Norden 1995), some exclusively so. Eickwort et al. (1981) indicate that nesting in pre-existing cavities is probably derived within the Megachilidae.

Difficulties in associating males and females in several groups of bees sometimes arise due to sexual dimorphism, and the comparatively ephemeral nature of males (Michener 2000). Unless specimens are collected and reared from nests (i.e., trap-nesting) or are caught during copulation, matching conspecifics of a given species is usually based on higher taxonomic classification, morphological similarities, geographic overlap, and speculation. Despite numerous studies, many North American bees are known from only one sex (Mitchell 1960), including 37% of described *Megachile* species (Table 1), and as a result the number of valid species for a given region may be significantly lower than suggested by catalogs (i.e., Krombein et al. 1979, Raw 2004). Because of their importance as pollinators, many bee collections are based on surveys from floral hosts which provide no knowledge of conspecifics, and other commonly used methods of mass collecting bees, such as Malaise traps and pan trapping, are equally problematic for similar reasons; although males do get collected, pairing them with their respective mates is not always possible. This issue is even more problematic for ground-nesting species (and their respective cleptoparasites); the nests of only a small proportion of these bees have been found or studied.

Molecular methods are commonly employed for analysis of bee phylogeny

(Pedersen 1996, Danforth 1999, Danforth et al. 2006 a and b), revealing cryptic species (Carman and Packer 1996, Packer and Taylor 1997, Hebert et al. 2004, Simmons and Scheffer 2004) and more recently have been advocated for accurate identification of organisms to species level (Hebert et al. 2003, Savolainen et al. 2005), including insects (Pinto et al. 2003). As such, molecular methods offer much hope for associating male and female conspecifics of sexually dimorphic organisms (Pilgrim and Pitts 2006).

### *Megachile* Subgenus *Megachile* Latreille s. str

The subgenus *Megachile* s. str. is a holarctic group found mostly in cool climates (Michener 2000), and five species are currently recognized in the western hemisphere (Mitchell 1935, 1962). *Megachile* s. str. are common members of temperate, boreal and subarctic North America, ranging from Nova Scotia (Sheffield et al. 2003) and Newfoundland through to Alaska and as far south as Mexico (Mitchell 1962). The North American species are *M. centuncularis* Linnaeus, *M. inermis* Provancher, *M. montivaga* Cresson, *M. nivalis* Friese and *M. relativa* Cresson; *M. centuncularis* has a holarctic distribution (Mitchell 1935, Michener, 2000) and is occasionally bivoltine in parts of its North American range (C.S. Sheffield, personal observations in Nova Scotia, Canada). Three species, *M. centuncularis*, *M. inermis* and *M. relativa* are collected commonly in trap-nest surveys within Canada and the northern United States (Stephen 1956, Medler 1959, Fye 1965, Kronic and Salt 1971, Ivanochko 1979, Sheffield 2006). In recent trap-nest surveys in Nova Scotia (Sheffield 2006), these three species accounted for 3.6%, 13.8% and 21.4% of all bees collected, respectively, surpassed only by *Osmia tersula* Cockerell (Osmiinae). *Megachile inermis* also has been recorded nesting in decaying wood (Mitchell 1935, Stephen 1956). *Megachile montivaga* differs from

Table 1. North American species of *Megachile* (Hymenoptera: Megachilidae) known from only one sex, and suggested conspecific or synonymy.

Subgenus	Species, author	Described sex		Suggested conspecific or synonym
		Female	Male	
<i>Argyropile</i>	<i>asterae</i> Mitchell	♀		
	<i>rossi</i> Mitchell	♀		
	<i>sabinensis</i> Mitchell	♀		
	<i>tulariana</i> Mitchell	♀		
<i>Chelostomoides</i>	<i>cartagenensis</i> Mitchell		♂	
	<i>subspilotulata</i> Mitchell	♀		
<i>Megachile</i>	<i>nivalis</i> Friese	♀		
<i>Megachiloides</i>	<i>alamosana</i> Mitchell		♂	
	<i>anograe</i> Cockerell	♀		
	<i>boharti</i> Mitchell	♀		
	<i>bradleyi</i> Mitchell	♀		
	<i>bruneri</i> Mitchell		♂	♂ of <i>M. hilata</i> Mitchell
	<i>coloradensis</i> Mitchell	♀		
	<i>dulciana</i> Mitchell	♀		
	<i>hilata</i> Mitchell	♀		♀ of <i>M. bruneri</i> Mitchell
	<i>hookeri</i> Cockerell	♀		Possible syn. of <i>M. nevadensis</i> Cresson
	<i>impartita</i> Mitchell	♀		
	<i>instita</i> Mitchell		♂	
	<i>inyoensis</i> Mitchell	♀		
	<i>lagumiana</i> Mitchell	♀		
	<i>latita</i> Mitchell	♀		
	<i>laurita</i> Mitchell	♀		
	<i>macneilli</i> Mitchell		♂	
	<i>maurata</i> Mitchell		♂	
	<i>melanderi</i> Mitchell	♀		
	<i>micheneri</i> Mitchell		♂	
	<i>mojavensis</i> Mitchell	♀		
	<i>nelsoni</i> Mitchell	♀		
	<i>oslari</i> Mitchell	♀		
	<i>pagosiana</i> Mitchell	♀		
	<i>parksii</i> Mitchell	♀		
	<i>pseudolegalis</i> Mitchell		♂	
	<i>pseudonigra</i> Mitchell	♀		
	<i>seducta</i> Mitchell	♀		
	<i>semilaurita</i> Mitchell	♀		
	<i>stoddardensis</i> Mitchell		♂	
	<i>subanograe</i> Mitchell	♀		
	<i>sublaurita</i> Mitchell	♀		
	<i>toscata</i> Mitchell	♀		
	<i>victoriana</i> Mitchell		♂	
	<i>wyomingensis</i> Mitchell		♂	
	<i>yumensis</i> Mitchell	♀		
<i>Neochelynia</i>	<i>aegra</i> Mitchell		♂	♂ of <i>M. chichimeca</i> Cresson
	<i>chichimeca</i> Cresson	♀		♀ of <i>M. aegra</i> Mitchell
<i>Pseudocentron</i>	<i>morio</i> Smith	♀		Possible form of <i>M. pruina</i> Smith
	<i>pruina nigropinguis</i> Mitchell	♀		
<i>Sayapis</i>	<i>dentipes</i> Vachal		♂	
	<i>helianthi</i> Cockerell	♀		
	<i>pugnata pomonae</i> Cockerell	♀		
<i>Xanthosarus</i>	<i>gemula cressonii</i> Dalla Torre	♀		
	<i>giliae</i> Cockerell		♂	♀ known, but not described



other members of the subgenus in that it lacks the mandibular cutting edges (Fig. 1) and uses flower petals for nest cell construction (Mitchell 1935, Michener 2000). Unlike the preceding three species, *M. montivaga* does not appear to accept trap-nests and instead nests in pithy plant stems as well as in soil (Ivanochko 1979). Mitchell (1935) indicates variability in nesting site choice/substrate for these four species.

In contrast to the preceding species which range as far south as Texas and Mexico, *M. nivalis* appears to have a more northern distribution (Mitchell 1935, 1962, Ivanochko 1979, Krombein et al. 1979). Little is known about its nesting biology but apparently females have been excavated from a river bank in the Yukon Territory in Canada along with other *Megachile* species: *M. giliae* Cockerell (♂'s only), *M. montivaga*, *M. relativa*, and *M. frigida* Smith (Ivanochko 1979). Males of *M. nivalis* have never been described (Mitchell 1935, 1962, Ivanochko 1979). Mitchell (1935, 1942, 1962) and Ivanochko (1979) indicate the similarity of female *M. nivalis* to *M. relativa* (and to a lesser extent, *M. centuncularis*), the main distinguishing characters being differences in the color and length of the pubescence on T6, and the color of the scopal hairs on S6 (Mitchell 1935, 1962, Ivanochko 1979); *M. nivalis* females are also generally larger than those of *M. relativa* (Mitchell 1942). Mitchell (1942) suggested that *M. nivalis* may represent a race of *M. relativa*, and speculated that the male would be very similar to that of *M. relativa* (Mitchell 1935). He subsequently (Mitchell 1942, 1962) examined specimens of male *Megachile* (not collected in copula) and suggested they may be related to female *M. nivalis*. However, he could not distinguish these males from those of *M. relativa* (Mitchell 1962).

*Megachile giliae*, with no described female (but with a northern distribution that overlaps with that of *M. nivalis*) has been indicated as the possible conspecific of *M. nivalis* (Mitchell 1935, Ivanochko 1979), but

this association seems unlikely since morphologically, it classifies within the subgenus *Xanthosarus* (Mitchell 1935, Krombein et al. 1979 as subgenus *Delomegachile*). However, the female of *M. giliae* has been collected and identified (see McGuire 1993, Bishop and Armbruster 1999), although no published descriptions presently exist.

In 2005, a trap-nest survey conducted in Yellowknife, Northwest Territories yielded many female *M. nivalis*, ten specimens of a male *Megachile*, and a male and female of the cleptoparasite, *Coelioxys funeraria* Smith (Megachilidae). Examination of genitalia (Figs 2, 3) and S5, S6 and S8 (Fig. 4) of *M. relativa* and the newly collected male specimens revealed similarities, but consistent and distinct differences were noted (see below). Additional differences between the Yellowknife males and *M. relativa* were observed on the lower genal area (Fig. 5), the clypeal margin (Fig. 6), and in wing venation (Fig. 7) – further details are provided below. These new specimens confirm the association of male *M. nivalis* with the female, and an updated key to the North American members of the subgenus *Megachile* s. str. is provided. The specimens are currently held in the senior author's collection, but material will also be placed in the Packer Bee collection, York University, Toronto, ON and the Canadian National Collection, Ottawa, ON upon completion of this study.

*Diagnosis of Megachile s. str.*—The body length of the subgenus varies considerably, from 7–20 mm (Michener 2000); *M. inermis* being the largest North American species. Females of *Megachile* s. str. can be separated from other North American subgenera by the five-dentate mandibles, with the fourth tooth separated from the inner tooth by a broad and shallow interspace which lacks a cutting edge (Fig. 1), including *M. montivaga*, although the indentation between the two inner teeth is obscure (Fig. 1a). *Megachile* s. str. females also have a single incomplete cutting edge in the second interspace (Fig. 1) which is some-

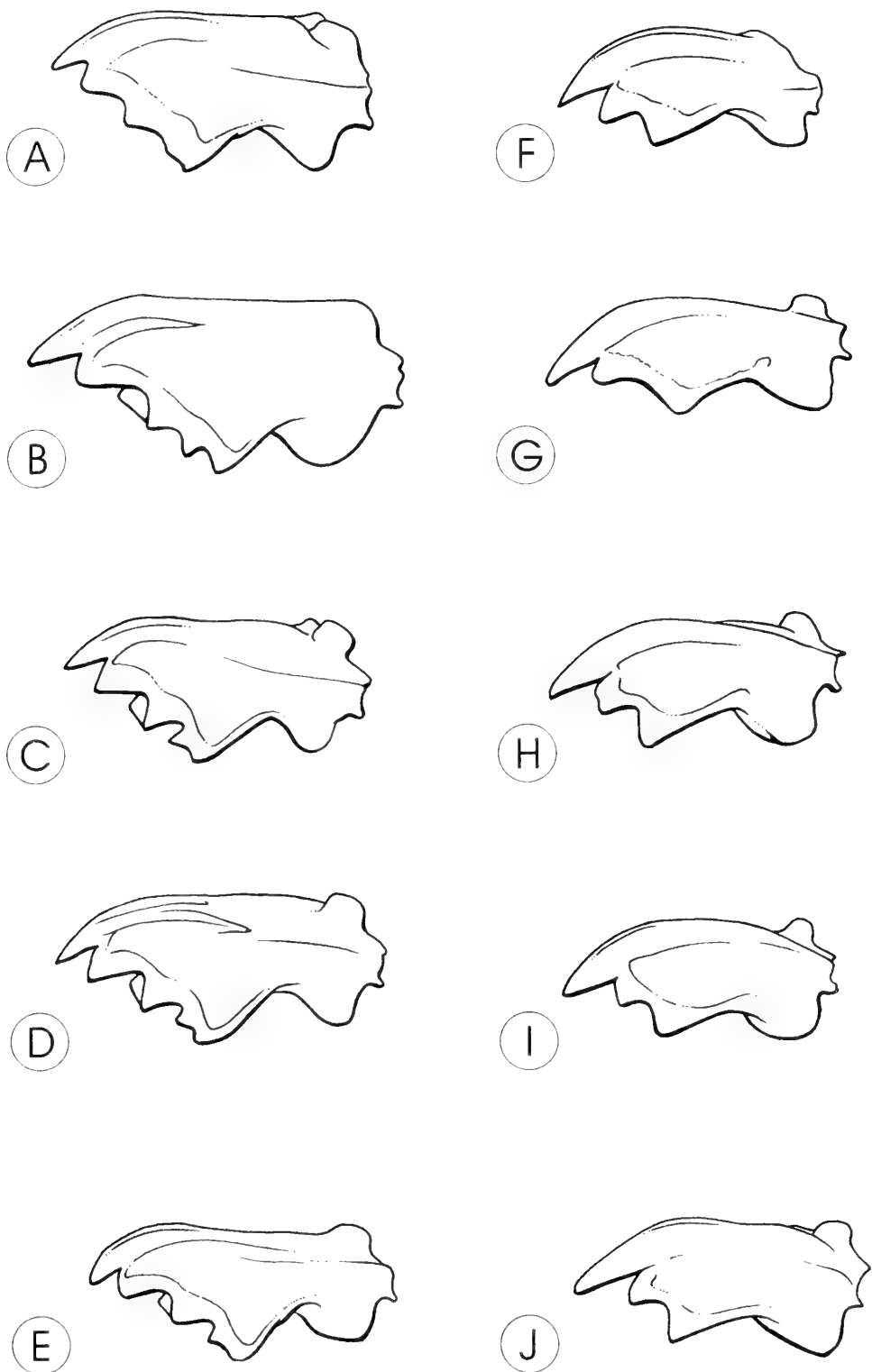


Fig. 1. Mandibles of female (left column) and male (right column) *Megachile* s. str.: *M. montivaga* (A and F); *M. inermis* (B and G); *M. centuncularis* (C and H); *M. relativa* (D and I); *M. nivalis* (E and J).

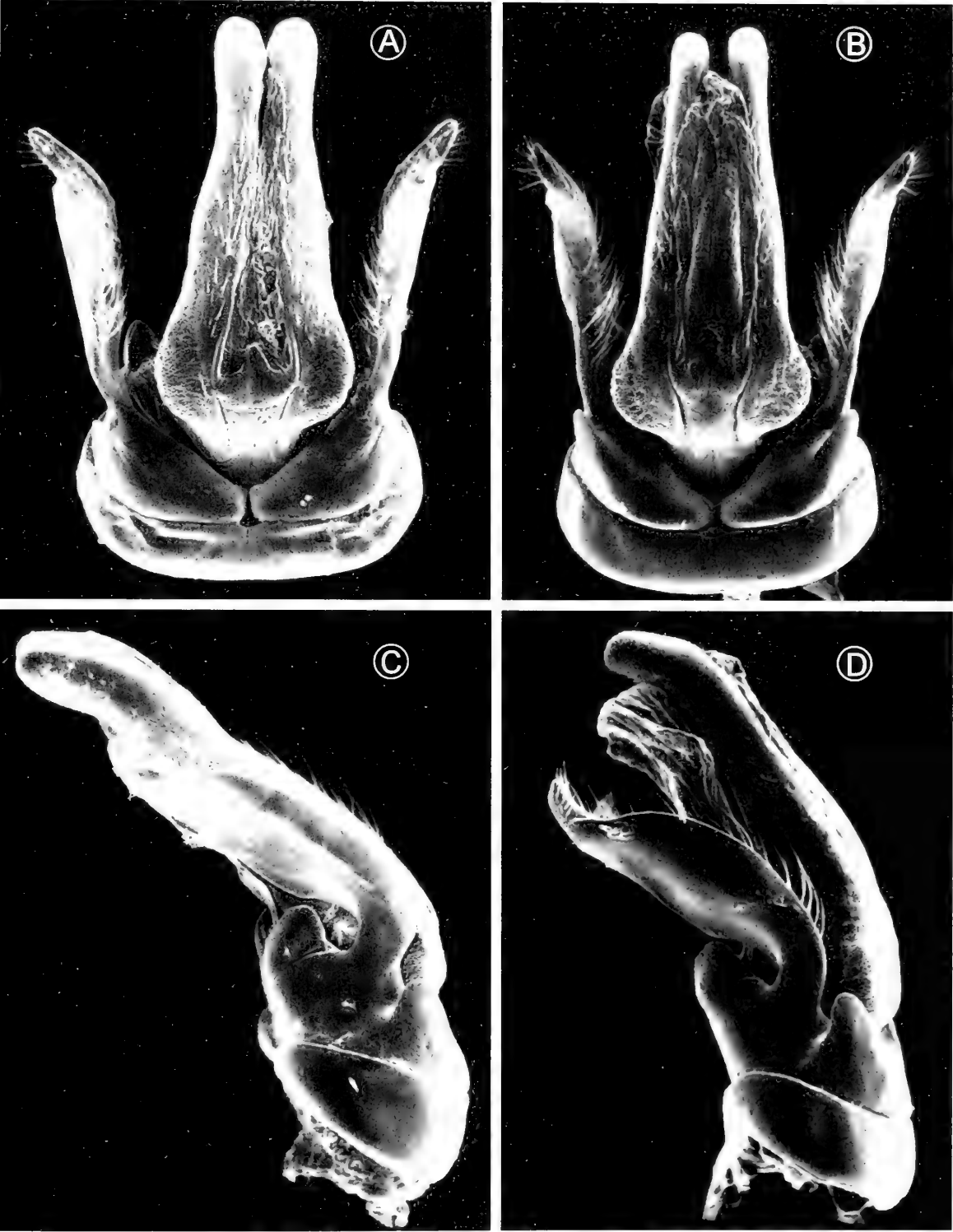


Fig. 2. Dorsal and lateral views of genital capsules of *Megachile relativa* (A and C) and *M. nivalis* (B and D).

what reduced in *M. relativa* (Michener 2000) and absent in *M. montivaga* (Fig. 1a). Female *M. montivaga* also differs from the other four species as T6 is concave in

profile, not straight. The scopal hairs are uniformly colored, ranging from fulvous to ochraceous; in *M. nivalis* the scopal hairs of S6 (and often S5) are black, not concolorous

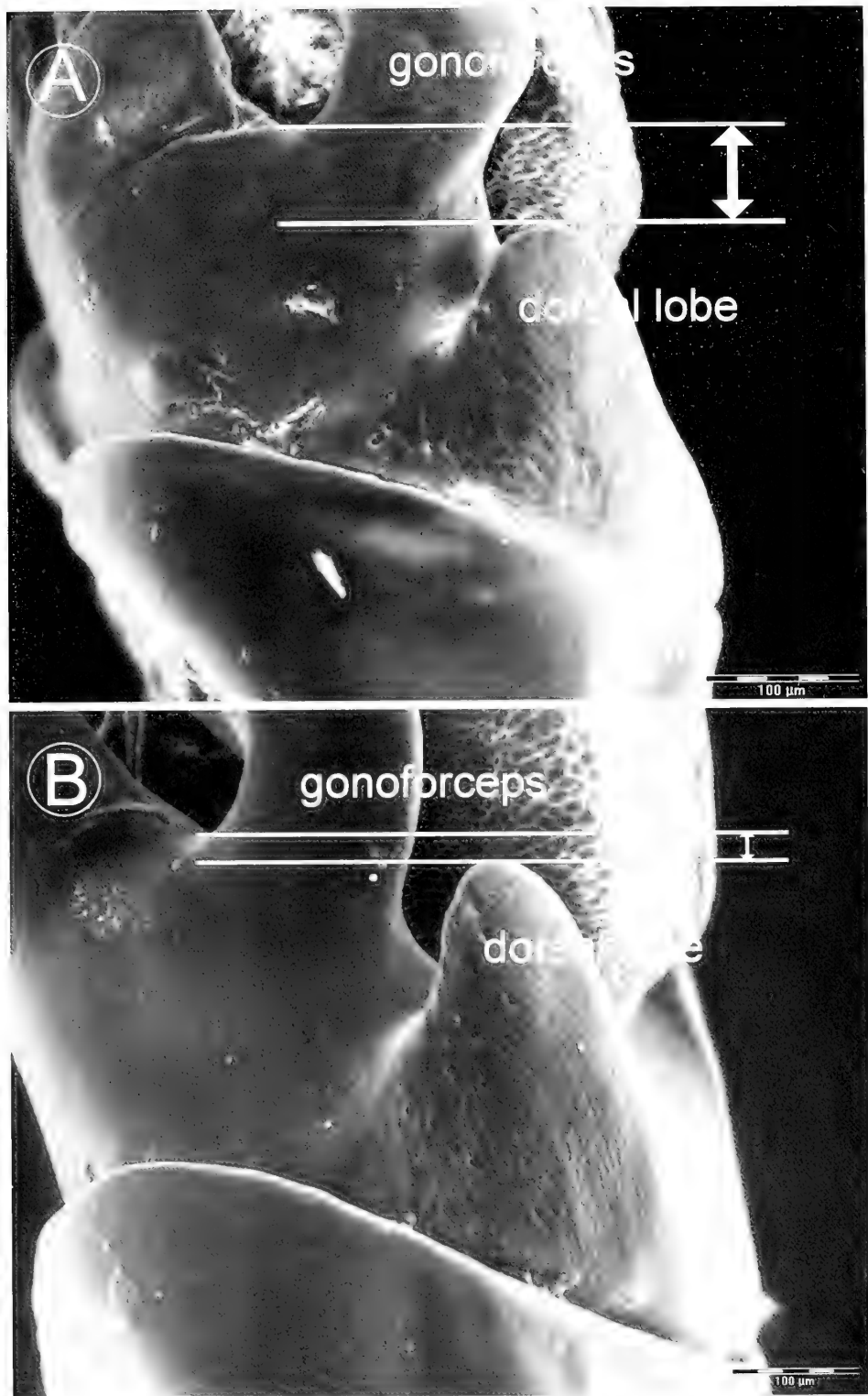


Fig. 3. Close up of lateral views of genitalia for *Megachile relativa* (A) and *M. nivalis* (B). Horizontal lines and double-ended arrows show relative length of dorsal lobe of gonocoxite to base of gonoforceps. Scale bars represent 100 µm.

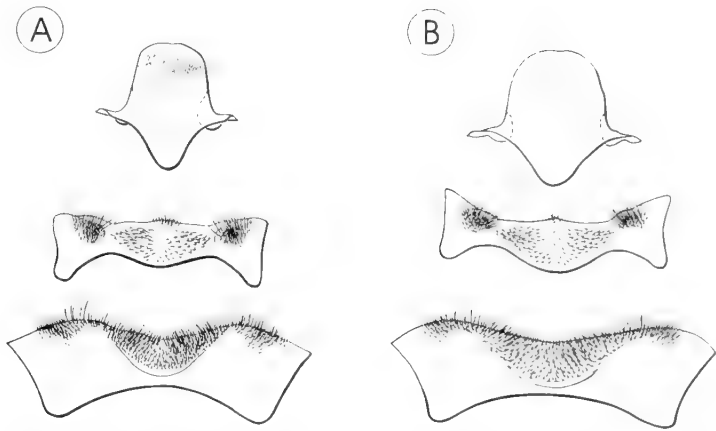


Fig. 4. Sterna V (bottom), VI (middle) and VIII (top) of male *Megachile relativa* (A) and *M. nivalis* (B).

with those of the preceding sterna which are ochraceous.

Males have three-dentate mandibles, and the teeth are equally spaced except in *M. inermis* (Fig. 1g). The mandibles also possess a narrow, distinct, basal or sub-basal, inferior process (Fig. 5a), the shape of the apical margin of this process varies slightly among species. The front coxa of male *Megachile* s. str. are hairy, with no spine and no patch of rufescent bristles, the exception being males of *M. montivaga* in

which the front coxal spines are present, represented by dentiform tubercles which are often difficult to see. Further descriptions of this subgenus can be found in Mitchell (1935), Ivanochko (1979), and Michener (2000). Descriptions of the North American species are found in Mitchell (1935, 1962) and Ivanochko (1979).

The subgeneric assignment of *M. montivaga* has come into question (Mitchell 1980, Michener 2000) due to the exceptions listed above. In addition, this species collects rose

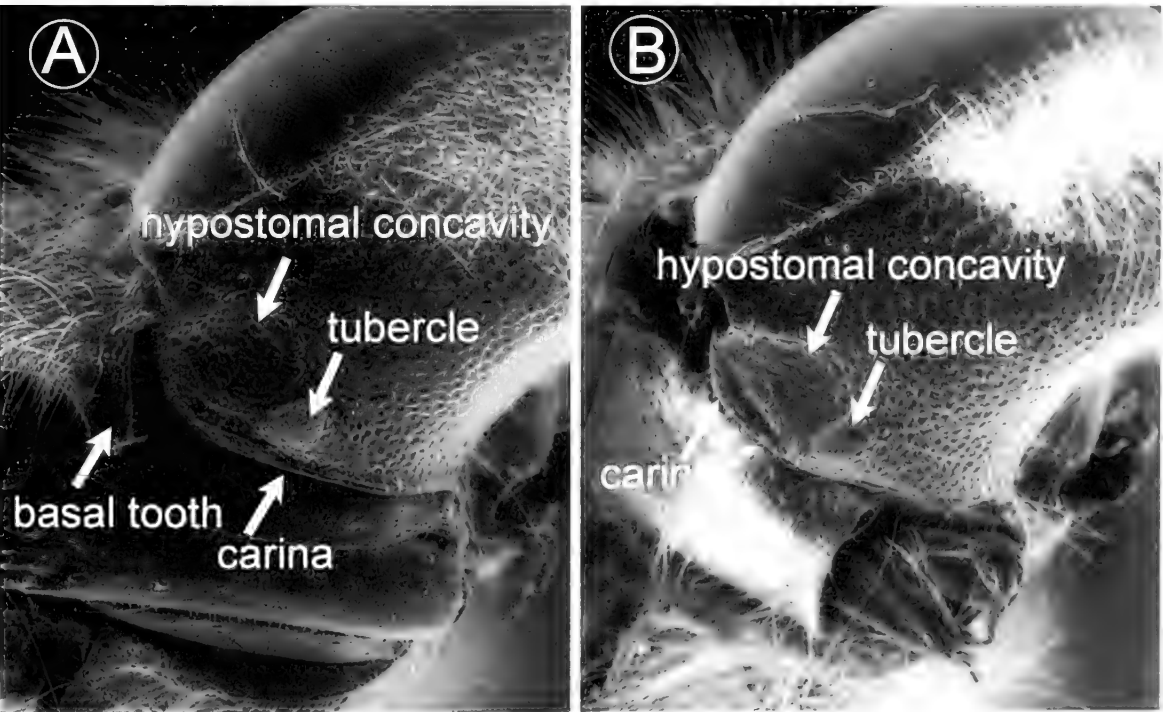


Fig. 5. The lower genal area of male *Megachile relativa* (A) and *M. nivalis* (B).

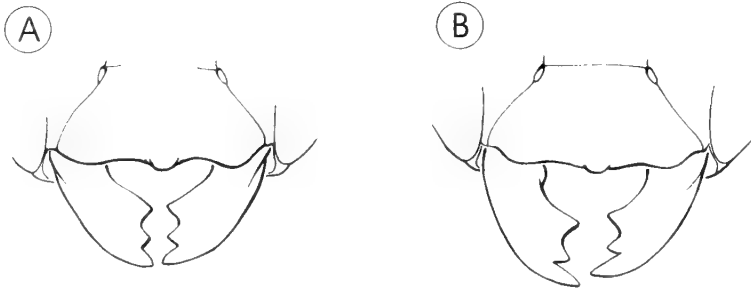


Fig. 6. Clypeal margins of male *Megachile relativa* (A) and *M. nivalis* (B).

petals instead of leaves for nest construction (Mitchell 1935, Michener 2000), and unlike the remaining four species, *M. montivaga* does not appear to accept trap-nests. Robertson (1903) proposed the generic name *Cyphopyga* just for *M. montivaga*. However, Mitchell (1935) indicated that the morphological differences were at the species level and had no real generic or even subgeneric

value, especially when the genitalia and hidden sterna of the males were considered. Despite this, he later (Mitchell 1980) recognized *Cyphopyga* as a four-toothed subgenus of *Megachile*, with *M. montivaga* as the only species, but Michener (2000) considered it unnecessary to recognize a unique supraspecific taxon for this species alone.

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KEY TO NORTH AMERICAN BEES OF THE SUBGENUS *MEGACHILE* LATREILLE S. STR.

The key provided is based on those provided elsewhere (Mitchell 1962, Ivanochko 1979) and through examination of specimens collected throughout Canada and currently held in the senior author's collection, and the Packer Bee collection, both at York University. The description of male *Megachile nivalis* is based on examination and dissection of the ten specimens collected in Yellowknife, NT in 2005. In mention of genitalia, gonoforceps refers to the distal (free) part of the gonocoxite plus the apical gonostylus.

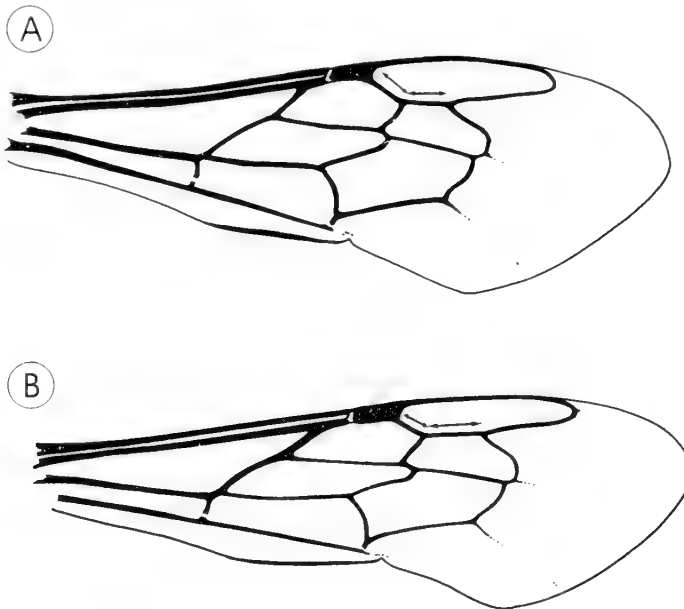


Fig. 7. Forewings of male *Megachile relativa* (A) and *M. nivalis* (B). Double ended arrows show the relative lengths of vein r (first submarginal cell) to Rs (second submarginal cell), r being much shorter in *M. nivalis*.

FEMALES

- 1
- a. Scopal hairs on S6 (and often S5) black

*nivalis* Friese
- b. Scopal hairs entirely pale fulvous or ochraceous

2
- 2
- a. T6 with a mixture of very short, suberect or appressed pubescence and abundant, long and erect pubescence which is visible in profile

3
- b. T6 with few erect hairs, showing mostly very short, sub-erect or appressed pubescence in profile

4
- 3
- a. Pubescence of T6 entirely dark

*centuncularis* Linnaeus
- b. T6 with erect and appressed golden tomentum

*relativa* Cresson
- 4
- a. T6 concave in profile; mandibles entirely lacking a cutting edge (Fig. 1a); punctures of clypeus and supraclypeal area coarse and close, interspaces much less than their diameter up to the edges of the distinct median impunctate line; interocellar distance subequal to distance of ocelli from edge of vertex; smaller species (<11 mm)

*montivaga* Cresson
- b. T6 straight in profile; mandibles with a distinct cutting edge in the second interspace (Figs 1b–e), surface of clypeus and supraclypeal area highly polished in central third, especially on apical ends, surface impunctate and/or with interspaces much greater than puncture diameter; interocellar distance much less than the distance from ocelli to edge of vertex; larger species (13 mm or more)

*inermis* Provancher

MALES

For users of Mitchell’s (1962) “Bees of the Eastern United States”, substitute couplets 2 and 3 below into his couplet 17 – page 113)

1.
- a. Distance from the apex of the middle tooth to the apex of the inner tooth nearly twice as great as the distance from the apex of the middle tooth to the apex of the outer tooth (Fig. 1g); interocellar distance much less than the distance from ocelli to edge of vertex; larger species (13 mm or more)

*inermis* Provancher
- b. Distance from the apex of the middle tooth to the apices of either the inner or outer teeth subequal (Figs 1f, h–j); interocellar distance subequal to distant from ocelli to edge of vertex; smaller species (<12 mm)

2
2.
- a. Clypeal margin with a distinct median tubercle (Fig. 6); surface of T6 polished above carina, the central punctures separated by their diameter

3
- b. Clypeal margin not tuberculate, but possibly narrowly produced medially (a few minute crenulations may also be visible medially in *M. montivaga*); surface of T6 either more closely punctate (the interspaces less than one puncture diameter) or surface tuberculate

4
3.
- a. Hypostomal tubercle short (Fig. 5a); hypostomal concavity shallow and not well defined (Fig. 5a); hypostomal carina distinct for most of its length (pile must be removed to see these features) (Fig. 5a); clypeal margin sinuous on either side of the prominent, shining, median tubercle (Fig. 6a); dorsal lobe of gonocoxite short, not attaining the base of gonoforceps (Fig. 3a), its length subequal to the width of gonobase (Figs 2a and c); vein r of the first submarginal cell normally subequal to vein Rs of the second submarginal cell (Fig. 7a)

*relativa* Cresson
- b. Hypostomal tubercle more prominent and wider at base (Fig. 5b); hypostomal concavity deeper and well defined; hypostomal carina interrupted by the hypostomal tubercle (Fig. 5b); clypeal margin slightly curved to nearly straight on either side of the less prominent, median tubercle (Fig. 6b); dorsal lobe of gonocoxite long, fully attaining the base of gonoforceps (Fig. 3b) and longer than the width of gonobase (Figs 2b and d); vein r of the first submarginal cell shorter than vein Rs of the second submarginal cell (Fig. 7b)

*nivalis* Friese



- 4. a. Coxal spines represented by dentiform tubercles; carina of T6 with a definite median emargination, apical margin of the segment with conspicuous inner teeth and spine-like lateral teeth, the surface above the carina dull, minutely rugoso-punctate ..... *montivaga* Cresson
  - b. Coxal spines entirely lacking; carina of T6 with an obscure median emargination, the apical margin of the segment with broad inner teeth and obscure lateral teeth, the surface above the carina with numerous small tubercles, the punctures very obscure ..... *centuncularis* Linnaeus
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*Megachile nivalis* Friese

*Megachile nivalis* Friese, 1903. Ztschr. System. Hym. Dipt. 3: 246. ♀  
*Megachile* (*Anthemois*) *santiamensis* Mitchell, 1934. Trans. Am. Ent. Soc. 59: 311. ♀  
*Megachile* (*Anthemois*) *nivalis* Mitchell, 1935. Trans. Am. Ent. Soc. 61: 174. ♀  
*Megachile* (*Anthemois*) *nivalis* Mitchell, 1942. Pan-Pacific Ent. 38: 15–16. ♀ (♂ misdet.)  
*Megachile* (*Megachile*) *nivalis* Mitchell, 1962. North Carolina Ag. Exp. Stat. Tech. Bull. 152: 129. ♀

Description of male presented here follows format used by Mitchell (1962).

*Male*.—Length 9–12 mm; entirely black except as follows: tegula testaceous along margins, basal tarsal segment black to somewhat reddened, following segments reddish testaceous; eyes slightly convergent below; clypeal margin nearly straight on either side of a distinct but small median tubercle (Fig. 6b); mandible three-dentate, with a rather narrow, sub-basal, inferior tooth which is subtruncate apically (Fig. 5a – *Megachile relativa*, but similar in structure); apical segment of flagellum slender and elongate; distance of lateral ocellus from margin of vertex and from margin of eye subequal; cheek somewhat broader than compound eye; punctures fine, slightly separated across vertex posteriorly, sparse between ocelli and eye, becoming close on cheek above and densely crowded or rugose below; face below ocelli rather coarsely rugosopunctate, becoming finely so below antennae and on clypeus; hypostomal depression well defined (Fig. 5b), hypostomal tubercle long and relatively prominent, broadly inter-

rupting hypostomal carina (Fig. 5b); pubescence golden, becoming paler on lower part of cheek, quite long and copious around antenna and lower part of face, on cheek below and on thorax laterally and posteriorly; vertex with an admixture of pale and black pubescence; mesoscutum and scutellum with more or less intermixed light and dark hairs which are quite long and erect but thin; mesoscutum dull, punctures close, shallow, not very coarse, slightly separated only in center of disc; punctures of scutellum slightly separated along mid-line, but otherwise quite uniformly close, those on axilla much finer and densely crowded; pleura dull, punctures shallow, quite close and poorly-defined; propodeum relatively smooth and shining; basitarsi quite short and slender; mid tibial spur short but well developed; tegula shining, rather uniformly, minutely and rather closely punctate; wings subhyaline, veins brownish, vein r of the first submarginal cell shorter than vein Rs of the second submarginal cell (Fig. 7b); T2–T4 shallowly grooved or depressed across base, basal margin of grooves not distinctly carinate, apical margins of terga depressed only toward sides, depressed medially only on T4 and T5, pale apical fasciae evident at extreme sides of the more basal terga, more or less complete on T4 and T5, discal pubescence rather thin, largely black but with pale hairs evident toward sides, length of discal pubescence exceeding apical margin of all terga when viewed laterally, basal tergum covered with copious, elongate, whitish pubescence; punctures very fine, surface

shining, close on T2 barely evident on T1, quite sparse on T3 and T4, becoming somewhat coarser laterally, but still well separated, T5 with somewhat closer and coarser punctures throughout; T6 shining, carina very low, broadly and shallowly incurved medially, punctures fine and close above carina, separated by their diameter, becoming somewhat more coarse and sparse laterally, inner teeth of apical margin broadly carinate, widely separated, relatively near the short, acute, lateral teeth; T7 quite prominent, broad and short, with a deep excavation on dorsal surface; S1–S4 exposed, closely but rather obscurely punctate, apical margins of S2–S4 broadly yellowish-hyaline and with thin, apical fringes of pale hairs; setose area of S5 restricted, finely setose (Fig. 4); S6 sparsely setose on each side, apical lobe barely evident (Fig. 4); gonoforceps slender with acute apex, gonocoxite basally with a distinct dorsal lobe which fully attains the base of gonoforceps (Figs 2 and 3).

*Distribution.*—The type locality for *Megachile nivalis* is Pikes Peak, Colorado (Mitchell 1935). This species is most common in northwestern areas of North America, having been reported from Alaska, Yukon Territory, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec. It is less common in the southern limits of its range which include Washington, Oregon, Idaho, Montana, Wyoming, Minnesota, and Colorado. It has also been reported from Maine (Mitchell 1962).

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## A Comparison of Pyrethrum Fogging and Screen-sweep Netting of Micro-Hymenoptera in Southern California Chaparral

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*Abstract.*—Three chaparral plant species, *Adenostoma fasciculatum* Hook. and Arn. (Rosaceae), *Ceanothus megacarpus* Nutt. (Rhamnaceae) and *Quercus berberidifolia* Liebm. (Fagaceae), were sampled for micro-Hymenoptera in the Santa Rosa Plateau Nature Reserve in Southern California. Two sampling methods of the shrub's canopy are contrasted: screen-sweep netting and pyrethrum fogging. Using both sampling methods and across all of the plant hosts, 242 species of Hymenoptera were collected. A total of 558 individuals and 173 species were collected by fogging, and 287 individuals and 115 species by screen sweeping. Although fogging captured more individuals and species, results were significant only for the number of individuals collected on *Quercus* and number of species on *Adenostoma*. On the three different plants, fogging sampled a similar or greater number of species than did screen sweeping. In terms of estimating species richness, fogging had an equivalent or greater efficiency than sweeping for collecting individuals and species. When combined with the labor efficiency involved in processing field samples, fogging is superior to screen sweeping. However, given the sample sizes within this study, both techniques are necessary, with the fogging technique sampling only 71.5% of the total number of species of Hymenoptera.

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Hymenoptera are one of the most diverse groups of insects, with approximately 115,000 described species and 300,000 to 2.5 million undescribed species (LaSalle and Gauld 1992, 1993, Gauld and Gaston 1995, Stork 1988, Grissell 1999). Based on conservative estimates, more than 10 percent of all insect species are parasitoids, and approximately 75% of these are Hymenoptera (Eggleton & Belshaw 1992). Recent estimates for Chalcidoidea alone estimate 357,000–400,000 species, of which only about 22,000 have been described (Noyes 1978, Noyes 2000, Heraty and Gates 2003). Parasitic Hymenoptera are valuable to agriculture as biological control agents (Van Driesche and Bellows 1996) and to conservation as a means of measuring biodiversity and a potential indicator of the diversity of lower trophic levels (Kremen et al. 1993, Heraty and Gates 2003).

Many of these parasitoids are small, usually ranging in size from 1–5 mm, and difficult to collect except with specialized methods (Noyes 1982, Noyes 1989). Various authors have attempted to evaluate the best methods to sample these micro-Hymenoptera with an emphasis on both numbers of individuals and species (Mason and Goulet 1981, Darling and Packer 1988, Noyes 1982, Noyes 1989, Buffington and Redak 1998).

Many studies have compared collecting techniques for Hymenoptera in tropical and temperate ecological regions (Henderson and Whitaker 1977, Noyes 1989, Gadagkar et al. 1990, Erwin 1995, Hill and Cermak 1997, Longino and Colwell 1997, Stork and Hammond 1997, Hoback et al. 1999, Yanoviak 2003), but little has been written about sampling in the short, dense, scrub vegetation that is typical of Mediter-

ranean climate zones. Use of an "Allen Vac" in a coastal sage scrub plant community in Southern California produced more individuals and a higher diversity of Hymenoptera than did sweep netting, and was considered more effective because insects were sampled from deeper within the shrub canopy than possible for a sweep net (Buffington and Redak 1998). The primary disadvantage of vacuum sampling is the damage caused to small, fragile parasitic Hymenoptera, which can make identifications difficult. Another important aspect for choosing a particular method is the amount of time spent sorting through the accumulated debris to find specimens (Southwood 1978). The efficiency of vacuum sampling is counterbalanced by the labor necessary to sort specimens from the accumulated debris collected along with the specimens. Unfortunately, sweep netting and the direct aspiration of minute specimens is probably the least efficient method of sampling – many specimens may simply escape during collection, avoid detection in the accumulated plant debris, or may not be sampled if they are not readily accessible by the net. Adding a metal screen to the net opening to exclude debris (Noyes 1982) can increase the efficiency of finding specimens, but this can result in greater damage to the specimens, and the efficiency of processing will depend on whether specimens are aspirated (maximizing loss of specimens) or if the entire sample of specimens and plant debris is collected into alcohol and later sorted in the laboratory (maximizing processing time). To improve the quality of specimens and reduce the time spent sorting, new methods for rapid assessment of Hymenoptera populations, and especially micro-Hymenoptera, in dense canopy situations are needed. Possible solutions include passive collecting techniques such as Malaise trapping (indirect method), pan trapping (indirect), or insecticide fogging techniques (direct method). These techniques yield fewer damaged specimens

and a limited amount of debris, but only the latter can be used to selectively sample specific plant hosts, as explained herein.

Canopy fogging techniques were reviewed by Erwin (1989), who noted that such techniques allow for sampling of tropical and temperate forest canopies more effectively than with other methods such as sweep netting. Problems with fogging in a tree canopy include collecting insects outside of the sampling area, drift of specimens from within the sampling area, and the need to collect at dawn, when there is no breeze, but perhaps less insect activity (Erwin 1989, Stork and Hammond 1997). Importantly, insects are collected somewhat randomly and can be sampled in replicated samples for a specific area (Stork and Hammond 1997). Insecticide fogging can also be applied to collecting insects on rough or inaccessible surfaces such as tree trunks (C. Burwell, pers. comm.) or vertical rock faces (S.B. Peck, pers. comm.). In a chaparral vegetation community, the issue is not whether sweeping can reach the upper canopy, but whether sweeping can efficiently and thoroughly sample insects from within the interior of the 'canopy' of dense, often thorny, bushes. Insecticide fogging of this miniature tree canopy has a potential for sampling a different array of insects in both numbers and species than would be sampled by beating the exterior of the shrub with an insect net. Canopy fogging is also an easily quantifiable method since a known surface area of catch basins can be put underneath the canopy being fogged. Canopy fogging in chaparral ecosystems might also produce samples that are free of debris or damage unlike screen-sweep netting. Another attribute of fogging is that it allows for the collection of specimens from individual plant species like screen-sweep netting. In this paper we hope to test the efficacy of pyrethrum fogging compared to screen-sweep netting in a chaparral ecosystem in Southern California for collecting parasitic micro-Hymenoptera.



Fig. 1. Fogging method used to collect Hymenoptera from a *Quercus berberidifolia* bush in Southern California.

## MATERIALS AND METHODS

*Location and date.*—Sampling took place on the two dates July 11, 2001 and July 18, 2001 at 3 adjacent sites in the Santa Rosa Nature Preserve, in Riverside County, California, at 33°31'N 117°14'W and 590 m elevation. We chose 3 similar stands of dense chaparral over a 5-acre area: one stand adjacent to a field of endemic bunch grass, the second adjacent to a road bordered by invasive grass, and the third in the heart of a dense stand of chaparral. We used both fogging and screen sweeping to collect from 3 individual bushes from 3 dominant plant species on two dates: *Adenostoma fasciculatum* Hook. and Arn. (Rosaceae), *Ceanothus megacarpus* Nutt. (Rhamnaceae), and *Quercus berberidifolia* Liebm. (Fagaceae).

*Screen-sweeping.*—We used a triangular net hoop with 38-cm sides and a recessed covering of 6.4-mm hardware cloth to exclude large debris. The sweep net was a fine-meshed net bag from Bioquip (Gardena, CA), with the apex of the net bag

open and held closed by a twist tie that could be removed to empty the contents into a 1-quart plastic Ziploc® bag containing 80% EtOH. The contents of the Ziploc® bag were rinsed with additional 80% EtOH to kill and preserve the insects. Each bush was swept over all its of the surfaces by a single collector (John Pinto, UCR) to keep the sampling as uniform as possible. Sampling of all 3 sites took about 45 min on each date.

*Fogging.*—The insecticide fogging of shrubs required several steps on the two dates. First, 36 yellow Dixie® bowls (total area = 1 m<sup>2</sup>) were placed underneath the canopy of each bush to be sampled. Each bush was sprayed with Raid Yard Guard® for 1 min from a distance of about 1.5 m, enveloping the bush in a fine fog with no visible droplets on the leaves (Fig. 1). Approximately one spray can (473 ml; 16 fl oz) was used for 3 bushes. After 5 minutes, pans were emptied and rinsed with 80% EtOH into one gallon plastic Ziploc® bags. Fogging took approximately



2 hours to complete from setup to finish for all 3 sites. The air movement was minimal during sampling periods and was not considered to have impacted specimen drift.

*Processing samples.*—Two strainers with square mesh openings of 3.2 and 1.6 mm were used to separate the screen-sweep samples into coarse, medium and fine debris samples. Because of the lack of debris, fogging samples were directly sorted without screening. Each sample was sorted with use of an 11×11-cm Rose Entomology® sorting tray with parallel sorting lanes separated by raised ridges 13-mm apart. To ensure that all specimens were discovered in the samples, each tray was sorted twice, and in some screen-sweep samples three times. Specimens were transferred to small glass vials and then dried for mounting by use of the Hexamethyldisilazane (HMDS) technique (Heraty and Hawks 1998) and then card mounted (Noyes 1982). All mounted specimens were individually labeled with collection information and a unique specimen identifier number. Data were input into a Filemaker® database for the UCR Entomology Research Museum, where all material was deposited. All Hymenoptera were identified to family, genus, and morphological species groups using available identification keys. Certain groups were identified, or our identifications verified, by other local specialists at UCR: Mymaridae identified by Serguei Triapitsyn, Trichogrammatidae by John Pinto, Pteromalidae and Eulophidae by Roger Burks, Signiphoridae by James Munro, Figitidae by Matthew Buffington, and Aphelinidae by Jung-Wook Kim.

*Data analysis.*—ANOVA analysis revealed no significant difference in specimens collected between sampling dates ( $p < 0.05$ ), so we pooled the data for the remaining analysis. A 2-tailed Student's *t*-test was used to compare the number of individuals collected by fogging and sweep netting for each family (Mendenhall

et al. 2003), the number of individuals in the two higher taxonomic groups (Chalcidoidea and non-Chalcidoidea) and families of Hymenoptera (Tables 1–3).

The ecological modeling program EstimateS version 7.0 (Colwell 2004) was used to compare the two methods for species richness (Figs 1–3) and similarity of shared species (Table 4) for Chalcidoidea and non-Chalcidoid micro-Hymenoptera by plant species. The diversity settings for EstimateS 7.0 were set to sample with replacement and the number of replications set to 1,000 to calculate the Chao1 richness estimator (Chao 1984), Sobs estimator (Colwell 2004) and singletons estimator (Chazdon et al. 1998, Colwell and Coddington 1994) (Figs 2–7). The advantage of estimating the diversity by selection of samples with replacement is that estimator variance remains meaningful at the right hand end of the accumulation curve, and thus can be used to compare data sets (Colwell 2004). Scatter plots of these estimator values of species were plotted against the estimated number of individuals observed in pooled quadrat samples to construct models (Figs 2–7). The Chao1 species estimator is used for the sampling history of species represented by at least two individuals (Magurran 2004). The Sobs estimator estimates sampling of the mean number of new species collected among the samples (Colwell 2004). The Singletons estimator estimates sampling of the mean number of new species represented only by one individual (Colwell and Coddington 1994), and thus is a rough estimate of the number of rare species. Accumulation curves from each of these estimators can be used to compare the relative efficiency of fogging and screen sweeping in capturing species diversity (Figs 2–7).

A Morisita-Horn species similarity index was calculated with use of standard default settings of EstimateS to compare the number of shared species collected on their respective plant species with fogging and screen sweeping after correcting for

Table 1. Mean number ± standard error (SE) (range and no. collected) of micro-Hymenoptera and morphospecies collected by fogging or sweep netting techniques at the Santa Rosa Reserve, California.

Plant type	Number of individuals		Number of species	
	Fog	Sweep	Fog	Sweep
	Total micro-Hymenoptera		Total micro-Hymenoptera	
<i>Adenostoma</i>	9.11±0.84 (3–18, 166)	4.61±0.19 (0–12, 82)	6.28±0.55* (2–11, 78)	3.61±0.51* (0–7, 40)
<i>Ceanothus</i>	6.56±1.16 (0–18, 117)	4.72±1.20 (0–18, 82)	5.39±0.75 (0–12, 56)	3.67±0.75 (0–13, 42)
<i>Quercus</i>	15.28±3.44* (0–46, 275)	6.89±0.96* (3–17, 123)	10.39±2.04 (0–28, 104)	6.00±0.82 (2–15, 67)
	Chalcidoidea		Chalcidoidea	
<i>Adenostoma</i>	5.67±0.66* (1–10, 102)	2.39±0.51* (0–7, 43)	4.7±0.53* (1–8, 52)	1.78±0.34* (0–5, 27)
<i>Ceanothus</i>	4.44±0.88 (0–9, 80)	3.83±1.09 (0–27, 69)	3.72±0.59 (0–9, 45)	3.17±0.98 (0–18, 31)
<i>Quercus</i>	11.11±2.65* (0–36, 200)	5.11±0.75* (0–12, 92)	7.28±1.55* (0–21, 71)	4.5±0.65* (0–11, 56)
	non-Chalcidoidea		non-Chalcidoidea	
<i>Adenostoma</i>	3.56±0.51 (1–9, 64)	2.17±0.58 (0–10, 39)	2.83±0.36 (1–6, 26)	1.61±0.38 (0–6, 13)
<i>Ceanothus</i>	2.06±0.35* (0–4, 37)	0.56±0.15* (0–10, 13)	1.78±0.28 (0–4, 11)	1.67±0.49 (0–9, 11)
<i>Quercus</i>	4.17±1.00* (0–15, 75)	1.72±0.34* (0–6, 31)	3.5±0.75* (0–10, 33)	1.56±0.26* (0–4, 11)

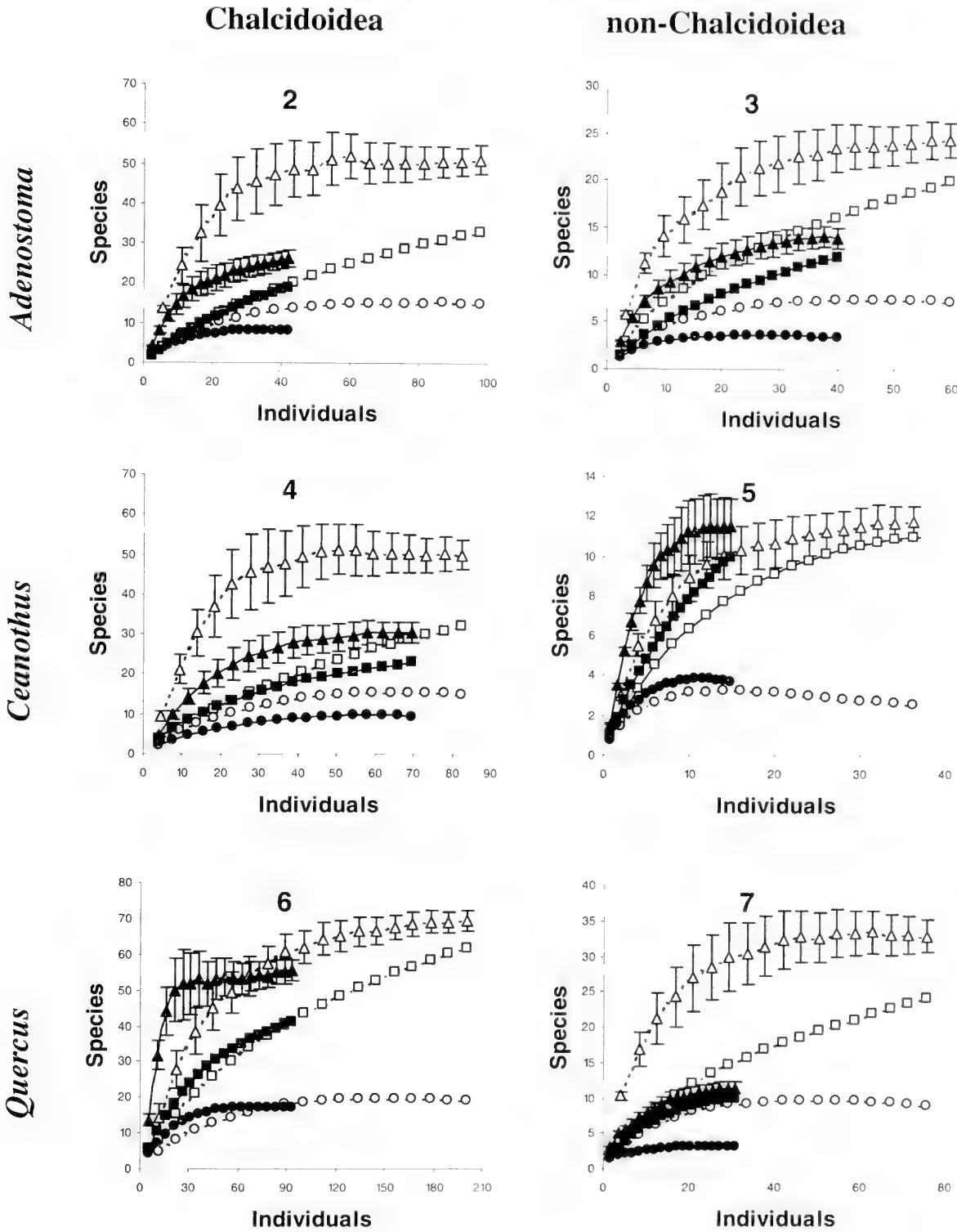
\*Significant within a category (Student's *t*-test, *p*<0.05). Values for the same categories were not significantly different between the 2 dates pooled but are significantly different between plant hosts (GLM ANOVA, *p*<0.05).

Table 2. Number of species collected by each sampling method (pooled) and average number of individuals (x ± SE) of Chalcidoidea sampled at the Santa Rosa Reserve.

	Number of species			Mean no. of individuals	
	Fogging	Sweeping	Both	Fogging	Sweeping
<b>Aphelinidae</b>	13	5	4		
<i>Adenostoma</i>				0.90 ± 0.20* (16)	0.33 ± 0.18* (6)
<i>Ceanothus</i>				0.61 ± 0.23* (11)	0.28 ± 0.14* (5)
<i>Quercus</i>				1.28 ± 0.40* (23)	0.50 ± 0.17* (9)
<b>Chalcididae</b>	1	0	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0.06 ± 0.06 (1)	0
<i>Quercus</i>				0	0
<b>Encyrtidae</b>	23	9	2		
<i>Adenostoma</i>				0.67 ± 0.21 (12)	0.28 ± 0.18 (5)
<i>Ceanothus</i>				0.61 ± 0.22 (11)	0.33 ± 0.14 (6)
<i>Quercus</i>				0.50 ± 0.33 (9)	0.17 ± 0.09 (3)
<b>Eulophidae</b>	29	25	7		
<i>Adenostoma</i>				1.24 ± 0.29 (30)	0.78 ± 0.25 (14)
<i>Ceanothus</i>				0.67 ± 0.23 (12)	0.50 ± 0.23 (9)
<i>Quercus</i>				1.50 ± 0.50 (27)	1.33 ± 0.31 (24)
<b>Eupelmidae</b>	3	5	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0.11 ± 0.08 (2)	0.06 ± 0.06 (1)
<i>Quercus</i>				0.06 ± 0.06 (1)	0.22 ± 0.02 (4)
<b>Eurytomidae</b>	2	2	0		
<i>Adenostoma</i>				0.06 ± 0.06 (1)	0.06 ± 0.06 (1)
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0.06 ± 0.06 (1)	0.06 ± 0.06 (1)
<b>Mymaridae</b>	3	1	11		
<i>Adenostoma</i>				0.61 ± 0.18 (11)	0.39 ± 0.14 (7)
<i>Ceanothus</i>				0.22 ± 0.10 (4)	0.33 ± 0.14 (6)
<i>Quercus</i>				1.17 ± 0.40 (21)	1.00 ± 0.29 (18)
<b>Ormyridae</b>	1	1	1		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0.11 ± 0.08 (2)	0.11 ± 0.08 (2)
<b>Pteromalidae</b>	14	3	6		
<i>Adenostoma</i>				0.39 ± 0.14* (7)	0.11 ± 0.08* (2)
<i>Ceanothus</i>				0.28 ± 0.14* (5)	0*
<i>Quercus</i>				3.61 ± 1.19* (65)	0.67 ± 0.21* (12)
<b>Signiphoridae</b>	0	1	2		
<i>Adenostoma</i>				0.11 ± 0.08 (2)	0
<i>Ceanothus</i>				0.28 ± 0.11 (5)	0.44 ± 0.15 (8)
<i>Quercus</i>				0.89 ± 0.77 (34)	0.78 ± 0.29 (14)
<b>Torymidae</b>	0	3	1		
<i>Adenostoma</i>				0	0.11 ± 0.08 (2)
<i>Ceanothus</i>				0	0.06 ± 0.06 (1)
<i>Quercus</i>				0.06 ± 0.06 (1)	0.06 ± 0.06 (1)
<b>Trichogrammatidae</b>	3	1	4		
<i>Adenostoma</i>				1.28 ± 0.39* (23)	0.33 ± 0.18* (6)
<i>Ceanothus</i>				1.61 ± 0.45 (29)	1.83 ± 0.64 (33)
<i>Quercus</i>				0.89 ± 0.30* (16)	0.22 ± 0.10* (4)
<b>Chalcidoidea</b>	92	56	38		
<i>Adenostoma</i>				5.67 ± 0.66* (102)	2.39 ± 0.51* (43)
<i>Ceanothus</i>				4.44 ± 0.88 (80)	3.83 ± 1.09 (69)
<i>Quercus</i>				11.11 ± 2.65* (200)	5.11 ± 0.75* (92)

Table 3. Number of species collected by each sampling method (pooled) and average number of individuals (x + SE) of non-chalcidoid Hymenoptera sampled at the Santa Rosa Reserve.

	Number of species			Mean no. of individuals	
	Fogging	Sweeping	Both	Fogging	Sweeping
<b>Bethylidae</b>	1	0	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0.06 ± 0.06 (1)	0
<i>Quercus</i>				0.17 ± 0.09* (3)	0*
<b>Braconidae</b>	7	1	0		
<i>Adenostoma</i>				0.33 ± 0.19* (6)	0*
<i>Ceanothus</i>				0.50 ± 0.22 (9)	0.06 ± 0.06 (1)
<i>Quercus</i>				0.33 ± 0.14* (6)	0*
<b>Ceraphronidae</b>	6	1	2		
<i>Adenostoma</i>				0.44 ± 0.18 (8)	0.39 ± 0.16 (7)
<i>Ceanothus</i>				0.06 ± 0.06 (1)	0.06 ± 0.06 (1)
<i>Quercus</i>				0.17 ± 0.12 (3)	0.06 ± 0.06 (1)
<b>Crabronidae</b>	1	0	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0.06 ± 0.06 (1)	0
<b>Figitidae</b>	3	1	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0.17 ± 0.09 (3)	0.06 ± 0.06 (1)
<b>Diapriidae</b>	1	0	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0.06 ± 0.06 (1)	0
<b>Dryinidae</b>	2	0	0		
<i>Adenostoma</i>				0.11 ± 0.08 (2)	0
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0	0
<b>Formicidae</b>	6	0	4		
<i>Adenostoma</i>				0.56 ± 0.17* (10)	0*
<i>Ceanothus</i>				0.44 ± 0.15* (8)	0*
<i>Quercus</i>				1.28 ± 0.39 (23)	0.78 ± 0.13 (14)
<b>Ichneumonidae</b>	1	0	0		
<i>Adenostoma</i>				0	0
<i>Ceanothus</i>				0	0
<i>Quercus</i>				0.06 ± 0.06 (1)	0
<b>Platygastriidae</b>	0	0	1		
<i>Adenostoma</i>				0.06 ± 0.06 (1)	0.28 ± 0.18 (5)
<i>Ceanothus</i>				0	0.06 ± 0.06 (1)
<i>Quercus</i>				0.11 ± 0.08 (2)	0.33 ± 0.20 (6)
<b>Scelionidae</b>	6	4	6		
<i>Adenostoma</i>				2.00 ± 0.46 (36)	1.50 ± 0.41 (27)
<i>Ceanothus</i>				1.00 ± 0.30* (18)	0.27 ± 0.11* (5)
<i>Quercus</i>				1.77 ± 0.55* (32)	0.50 ± 0.12* (9)
<b>Sphecidae</b>	1	1	0		
<i>Adenostoma</i>				0.06 ± 0.06 (1)	0
<i>Ceanothus</i>				0	0.11 ± 0.08 (2)
<i>Quercus</i>				0	0
<b>non-chalcidoid Hymenoptera</b>	35	8	13		
<i>Adenostoma</i>				3.56 ± 0.51 (64)	2.17 ± 0.58 (39)
<i>Ceanothus</i>				2.06 ± 0.35* (37)	0.56 ± 0.15* (10)
<i>Quercus</i>				4.17 ± 1.00* (75)	1.72 ± 0.34* (31)



Figs 2-7. Species accumulation curves generated by use of EstimateS 7.0 for the pooled fogging (open symbols) and sweep-netting (closed symbols) data. Triangles represent the Chao1 estimator, squares the Sobs estimator, and circles the singletons estimator.

Table 4. Morisita-Horn indices for shared species of micro-Hymenoptera collected at the Santa Rosa Plateau Reserve by canopy fogging and screen netting by plant host.

	Chalcidoidea	Non-Chalcidoidea
<i>Adenostoma</i>	0.69	0.73
<i>Ceanothus</i>	0.84	0.59
<i>Quercus</i>	0.75	0.63
Total	0.84	0.77

sample size (Table 4). The Morisita-Horn index has been shown to be robust and more reliable than other shared species indices because it is not strongly influenced by species richness and sample size (Wolda 1981, Magurran 2004).

RESULTS

Fogging of the plant canopy consistently collected more individuals and species than screen sweeping across the 3 types of plants sampled (Table 1). A total of 558 micro-Hymenoptera specimens were collected by fogging as compared to 287 by screen sweeping. Samples were significantly different only for the number of individuals of all micro-Hymenoptera from *Quercus* and the number of species from *Adenostoma* (Table 1). More individuals of Chalcidoidea (Table 2) and non-Chalcidoid micro-Hymenoptera (Table 3) were collected with fogging across all plants sampled. Use of fogging produced significantly higher numbers of Chalcidoidea on *Adenostoma* and *Quercus* (Table 2) and non-Chalcidoid micro-Hymenoptera on *Ceanothus* and *Quercus* (Table 3) than sweeping. In virtually all of the family level comparisons, use of fogging produced a greater number of individuals than did sweeping (Tables 2, 3). However, the differences were significant for only some Chalcidoidea (Aphelinidae, Pteromalidae and Trichogrammatidae) and other Hymenoptera (Bethyridae, Braconidae, Formicidae, Scelionidae). Except for Pteromalidae on *Quercus*, Aphelinidae and Trichogrammatidae were the most commonly

sampled wasps. Individuals of these families are minute and are likely most common in the interior canopy of the bushes where they attack sessile Hemiptera and eggs of various insects.

A total of 242 species of Hymenoptera were collected across all of the samples, with Chalcidoidea represented by 186 species (76.9%). For all species (micro-Hymenoptera, Chalcidoidea and non-Chalcidoidea), fogging consistently produced more species, on average, than screen-sweeping (Table 1) (173 versus 115 total species collected by each technique) and significantly more species on *Adenostoma* (Table 1). Significantly more species of Chalcidoidea were collected on *Adenostoma* and *Quercus*, whereas more species of non-Chalcidoidea were collected only on *Quercus* (Table 1). Each method did not always collect the same species. Only 38 species of Chalcidoidea and 13 species of non-Chalcidoid micro-Hymenoptera were sampled by both methods (Tables 2 and 3). Sweep netting collected an additional 56 species of Chalcidoidea (30.1%) and 8 species of non-Chalcidoid micro-Hymenoptera (14.3%) (Tables 2 and 3). As expected, because of the greater number of specimens collected fogging collected a larger proportion of additional species that were not collected by screen sweeping (92 species or 49.5% of Chalcidoidea; 35 species or 62.5% of non-Chalcidoid micro-Hymenoptera). When considering the unique species collected by a particular method, along with the species collected by both methods, fogging sampled 69.9% of the species of Chalcidoidea whereas screen sweeping sampled 50.5% of the species, and respectively 85.7% and 37.5% of the non-Chalcidoid micro-Hymenoptera. Because of different sample sizes obtained from each method (significantly more for fogging), an unbiased Morisita-Horn analysis estimated that the two sampling methods produced samples with 69–84% shared species of Chalcidoidea and 59–77% shared species of non-Chalcidoid micro-Hymenoptera (Ta-

ble 4). However, especially for Chalcidoidea, screen sweeping collected a large number of unique specimens (56) despite the low sample size.

Of the three estimators, Chao1 provides an indication of the ability to sample the species thoroughly (more than two individuals of each species sampled), Sobs focuses on the accumulation of new species, and the singletons estimator is the accumulation of species based only on a single specimen. Only the singletons estimator is expected to decline as a habitat is more thoroughly sampled and species are shifted to the Chao1 category. The Chao1 and Sobs estimates should both plateau as the number of species becomes thoroughly sampled. In all cases, estimates for fogging were consistently based on a sample with greater number of individuals (Figs 2–7; Table 1). Results for the Chao1 estimator species accumulation curve had the number of ‘common’ species both accumulate and also reach a plateau at a significantly faster rate using the fogging technique for most of the data partitions (Figs 2–4, 7), whereas screen sweeping accumulated common species at a faster rate for non-Chalcidoidea on *Ceanothus* (Fig. 5) and Chalcidoids on *Quercus* (Fig. 6). In these latter two cases, fogging still sampled more species overall on *Quercus* (71 versus 56), whereas the same number of species of non-Chalcidoidea (11) were sampled on *Ceanothus* and in neither case did the number of species appear to plateau (Figs 5, 6; Table 1). Thus fogging will generally sample the highest and best represented diversity of common species with the least effort, as based on the number of specimens collected. The mean number of new species accumulated (Sobs estimate) was virtually the same for Chalcidoidea using both methods (Figs 2, 4, 6), and for the non-Chalcidoid micro-Hymenoptera, slightly higher on *Ceanothus* (Fig. 5) or lower on *Adenostema* and *Quercus* (Figs 3, 7). The number of species represented by a single specimen (single-

ton) accumulated at a slightly faster rate in most of the fogging samples (Figs 2–4, 7), but were roughly the same for the *Ceanothus* non-Chalcidoidea (Fig. 5) and *Quercus* Chalcidoidea (Fig. 6). Only the non-Chalcidoid micro-Hymenoptera on *Adenostema* (Fig. 5) demonstrated a decline in the number of singletons, suggesting overall that the maximum number of species had been sampled even though the species accumulation curves (Chao1 and Sobs) had not yet reached a plateau.

## DISCUSSION

Insecticide fogging of tree canopies has been experimented with since the late 1960's (Martin 1966, Gange and Martin 1968, Roberts 1973, Erwin and Scott 1980, Erwin 1983, Adis et al. 1984, Stork and Hammond 1997). Typical canopy fogging in the tropics is used to access the forest canopy 30–60 m above the ground (Erwin 1983, Stork and Hammond 1997). Here we suggest that the canopy of dense thorny shrubs in chaparral habitat can present some of the same problems of sampling, but on a much smaller scale. The fogging strategy employed in this paper has a number of advantages in: 1) relying upon compact and inexpensive equipment that can be carried easily to the field, 2) the sampling area can be defined by the collecting surface under the plant, 3) a specific bush or species of plant can be targeted, 4) debris is minimized and the specimens can be quickly and efficiently processed, 5) there is very minimal, if any, damage to specimens, and 6) there is no damage to the plants being sampled, which may be a factor in some conservation studies. Our method draws many parallels with the typical tropical forest canopy fogging as in Stork and Hammond (1997), and faces similar issues of specimen drift within and outside of the sampling area, but on a less dramatic scale. Climatic conditions (i.e. wind) remains an important factor, but can be monitored and controlled throughout the



sampling period, and sampling can be done during presumed periods of peak insect activity. Typical chaparral shrubs stand waist high and thus access to the canopy is not a problem, and fogging of chaparral or similar shrub canopies may allow access to this seldom collected niche.

Noyes (1989) demonstrated variable results when comparing sweep netting to canopy fogging of trees in the tropical forests of Sulawesi, but did not speculate as to which was more effective at collecting parasitic Hymenoptera. Noyes (1989) argues that each method of collecting will have its own advantages over another, but this may relate to sampling different ecological niches, more than the overall efficiency of collecting the same niche. We observed this within our study, in which fogging sampled only 71.5% of the Hymenoptera and screen sweeping sampled only 47.5%. A large number of species were represented by only one or two specimens, and the differential sampling may be due to a different distribution of species on the individual host plants being sampled. The only way to account for this would be to increase the number of plant hosts being sampled in order to decrease the variance in species being sampled; however, this would dramatically increase the effort for sampling with the screen sweep method.

In this study, insecticide fogging sampled a greater or equivalent number of individuals and species of micro-Hymenoptera as compared to sweep netting in a chaparral ecosystem (Tables 1–3, Figs 2–7). Similar to vacuum sampling, the difference was likely because of greater access to wasps within the interior shrub canopy (Dietrick et al. 1960, Buffington and Redak 1998). Sweep netting generally samples insects from the tops and sides of the shrub canopy (Southwood 1978, Buffington and Redak 1998). Differences in the shrub architecture may have led to some of the variability in the effectiveness

of fogging versus screen-sweeping (Table 1, Figs 2–7). Both *Quercus berberidifolia* and *Adenostoma fasciculatum* have dense overhanging canopies that the screen-sweep net could not penetrate. However, *Ceanothus megacarpus* has a sparse willow-like canopy architecture and the screen-sweep net could be used to sample most of the canopy. Thus, when sampling dense chaparral shrubs, canopy fogging would have an advantage over screen sweeping at capturing a greater diversity of micro-Hymenoptera. When sampling open shrubs, no difference in the wasps being sampled by either method is expected.

Insecticide fogging, coupled with the collection of specimens into pans of a defined size, allowed for better quantification of the capture of wasps in a defined area, with 1 m<sup>2</sup> being the combined area of the pan traps placed under each shrub. This is somewhat similar to the multiple 1 m<sup>2</sup> funnel sampling method employed in canopy fogging of tree canopies (Stork and Hammond 1997), although we did not treat each pan as a separate sampling unit because of the expected low sample size. Sampling by screen sweeping is more arbitrary, being based on the number of sweeps using an undefined arc, velocity, and the area sampled (Southwood 1978). It is possible to define the area sampled through screen sweeping by the size of the shrubs being sampled, which in this study certainly had a surface area greater than 1 m<sup>2</sup>, but each shrub varied substantially in size. Other factors that mitigate against screen-sweeping are collector bias in sweeping efficiency and potential damage to the host plants by intensive sweep netting.

The efficiency of processing samples is an important factor. More time was spent in the field setting the pans under each shrub, fogging the canopy, and collecting specimens from the pans. However, the fogging technique produced samples almost entirely free of debris, which allowed

for specimens to be easily located and processed. Fogging could theoretically allow for more samples to be taken, which overall is the best way reduce the variance in samples from natural habitat (Southwood 1978).

It is difficult to compare trapping methods directly for numbers of individuals and species when, because of the method, they are not comparable for a similar investment of effort. Modeling of trap catches through various resampling methods allows for an estimate of whether the diversity and quota of specimens can reach the same asymptote, the relative efficiency of reaching that value, and whether a particular method has already reached that estimated value. In almost all cases, fogging was estimated to collect more species and at a faster rate than sweep netting (Figs 2–3, 5–7). Only on *Ceanothus* was the diversity of non-Chalcidoidea estimated to be equal and the number of species accumulated at a faster rate with screen sweeping (Fig. 5). The upright growth and open canopy of *Ceanothus* may allow for an equal number of individuals and species to be sampled by both methods. The Morisita-Horn shared species index (Table 4) indicates that the use of both fogging and screen sweeping sampled similar species of Hymenoptera (59%–84% similarity), with no bias in groups. Thus, when corrected for sample size either method would sample approximately the same groups of species in a chaparral ecosystem.

The goals of sampling parasitic Hymenoptera in different habitats are endless. Here we were interested in sampling numbers of individuals and species from isolated plants in a dense shrub canopy in chaparral habitat at a single point in time. This is a diverse ecosystem, with 242 species collected on only two sample dates. The same or more individuals were sampled from each plant using fogging as compared to screen sweeping. In terms of specimen quality, efficiency and quantification, insecticide fogging, with collection

of specimens into circular pans placed under the shrub canopy, is a superior technique over both screen sweeping and vacuum sampling.

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## **Marjorie Chapman Townes 28 March 1909–8 October 2006**

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Marjorie Chapman Townes, 97, of Timberhill Place, Corvallis, Oregon, died 8 October 2006.

She was the widow of Henry Keith Townes, Jr., who died in 1990.

Born in Pawcatuck, Connecticut, on 28 March 1909, she was the daughter of the late William Robinson Chapman and Winifred Naomi Brown Chapman.

Marjorie attended Westerly, Rhode Island public schools and was Valedictorian of her class at Westerly High School in 1927. She then attended Mt. Holyoke College, from which she graduated "Cum Laude" with a BA in Botany in 1931, a member of Phi Beta Kappa honor society. Marjorie completed her MA in Botany at Cornell in 1932 with a thesis on the anatomy of Witches' Broom and her PhD in 1933, with a dissertation on the floral anatomy of Berberidaceae. She then taught Biology at Mt. Holyoke College during 1935–1937.

On 7 October 1937, she married entomologist Dr. Henry Townes from Greenville, South Carolina, whom she had met at Cornell. The young couple lived in Syracuse, New York, for a year, where her husband taught at Syracuse University and where their son David was born, then two years at Ithaca, New York, while her husband taught at Cornell University. They next lived a year in Philadelphia, Pennsylvania, where their daughter Jean was born, and as Henry conducted research at the Academy of Natural Sciences, then in Takoma Park, Maryland (1941–1948), and McLean, Virginia (1948–1949),

while he was employed by the U.S. Department of Agriculture in Washington, D.C. as a research taxonomist. From 1949 to 1952, they lived in Raleigh, North Carolina, while Henry taught at North Carolina State University and investigated tobacco pests. During 1952–1954, they lived in Manila, The Philippines, where Henry served as an Advisor to the Philippine Department of Agriculture concerning pests of rice and corn. They then moved to Ann Arbor, Michigan (1956–1985), where they worked together on various research projects concerning Hymenoptera, supported by grant funds, and Henry occasionally taught at the University of Michigan and Michigan State University. While in Ann Arbor, they established the American Entomological Institute as a not-for-profit organization to manage the huge, world-class Hymenoptera collection and library that the two of them had by then amassed. In 1985, they moved the Institute to Gainesville, Florida, operating it as a private organization supported by grants and endowment income. After Henry died in 1990, Marjorie moved to Eugene, Oregon, to be near her daughter Jean, later moving to Corvallis in 2003, to be even closer.

Marjorie and Henry were a remarkable research team. She published 14 monographs with him mostly concerning parasitic wasps (see below). Together they undertook numerous entomological expeditions to many countries around the world and prepared the resulting specimens for further scientific study. The

Institute began to publish books and research articles in the 1960s, for which Marjorie undertook responsibility for subscription and sales. Her work on the labelling and arrangement of the Institute's collection was indispensable, and contributed to its consisting of 900,000 specimens by 1990. Together, the Townes were appreciated internationally as a team who contributed significantly to our understanding of the taxonomy of Hymenoptera, especially of the family Ichneumonidae.

Marjorie is survived by her son David Townes of New York City, New York, and her daughter Jean Townes of Corvallis, Oregon, and by her grandchildren Andrew (28), Edward (20), Alice (19), and Catherine (16).

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Jean Townes, Covallis, OR  
John Morse, Pendleton, SC

*Several scientists, mostly those who knew her and who are now members of the Board of Directors of the AEI, have shared some of their reflections about Marjorie:*

“Several nights ago I was working late, making a list of Neotropical ichneumonids as part of setting up a research project for a beginning graduate student. As I extracted information from several of the catalogs published by the AEI in the Sixties, I was struck by the realization – and not for the first time – of how much of this was the result of Marjorie’s labor. She was not a simple amanuensis. Although the scientific content was Henry’s, an enormous amount of the arrangement, editing, and the like was due to Marjorie. She accompanied Henry to museums and went out into the field for extended trips, both foreign and domestic. The assemblage of the AEI collection would have been

severely curtailed if not for her careful and assiduous labeling, and assistance with myriad curatorial tasks. In short, the modern ichneumonid enterprise would be very different if Marjorie had taken another branch of life's road.

"While 'the modern ichneumonid enterprise' is a fairly obscure branch of science, those of us involved with it believe in its importance. This group of wasps is enormous in both numbers of individuals and species, and we think that its study is necessary: both from a practical aspect (pesticide-free insect control and the like) and for a better appreciation of fellow travelers on this planet. Henry and Marjorie thought so too, and devoted their lives to building up an unique resource and study center.

"Marjorie's labors are used every day in the form of examined specimens and consulted publications. Her life touches each of us constantly and will continue to do so as long as the entomological endeavor continues." – Dr. David Wahl, *American Entomological Institute, Gainesville, Florida*.

"My first visit to the Townes' house was sometime in the early 1980s in Ann Arbor. Although I enjoyed getting direction and advice from Henry I can't remember any details of my interactions with him on that visit. What I do remember the most is Marjorie, and three things come to mind: the wonderful cookies that she made for our coffee breaks, her unique call, sort of like a whistle but not quite, that was used to call us for lunch and breaks, and her feeding of the birds outside of the window where I was working. These things may seem trivial but obviously they are not. Marjorie brought warmth and charm and made my visit delightful. I had other visits to Ann Arbor and many more to Gainesville; Marjorie was always gracious and full of energy. In later years, when Henry was ailing, Marjorie's bright personality obscured the difficulties that they were facing. I think of Marjorie often and I'm glad that the genus of braconid wasps,

*Marjoriella* that I named after her is so difficult to place in the tree of life. It is beautiful, rare, and enigmatic, much like its namesake. She will be missed by the many, many scientists who had the great fortune to be touched by her." – Dr. Michael Sharkey, *University of Kentucky*.

"My recollections of Marjorie Townes:

"First, as a scientist, she ably assisted Henry in the publication of his descriptive work. I had an opportunity to observe this directly on some of Henry's later publications, where Marjorie read the descriptions out to Henry as he mentally proofed them. As one who has proofed hundreds of articles, I can attest to the tremendous efficiency of this method. Proofing your own articles is a difficult task. Marjorie's expert assistance saved many hours and also improved the quality of the end-product as she would catch small typos and other errors that are easily overlooked when reading your own work. She also managed, as far as I could determine, the AEI publications, which was a pretty amazing achievement when you consider that the AEI publications routinely made more money than most periodicals.

"Earlier in Henry's career, Marjorie co-authored several publications and justifiably so. She took an active part in all phases of the research, giving up her own area of training and expertise to provide full support to Henry's endeavors. Additionally, she assisted Henry in mounting newly acquired material and took over most of the duties labeling these accessions. In essence, Marjorie served as combination technician and fellow researcher. Without her very real contributions to AEI, Henry would not have been able to accomplish nearly as much as he did.

"For a period of about a decade (or maybe a little more), I regularly visited the AEI as part of my taxonomic research, often staying one or two weeks at a time, and on several occasions accompanied by my wife and young daughters. While Henry was a wealth of information and



graciously allowed me full access to the collections, it was Marjorie who made us feel most welcome as visitors, opening up their home as a place for us to stay and, perhaps most importantly, assuring a return visit on our part. From my perspective, the extensive use of the AEI resources by scientists during that period was in large part due to the welcoming atmosphere that Marjorie was responsible for."

– *Dr. Bob Wharton, Texas A&M University, College Station, Texas.*

"I once received a shipment of specimens from the AEI that were packed in an assortment of colored foam peanuts. Marjorie had included a little note: 'just like a party, isn't it!' She was a very nice and kind person and will be greatly missed." – *Dr. John Heraty, University of California, Riverside.*







## INSTRUCTIONS FOR AUTHORS

**General Policy.** *The Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are acceptable if the species has economic importance or provides new data on the biology or evolution of the genus or higher taxon. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level. All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript. The language of publication is English. Summaries in other languages are acceptable.

**The deadline for receipt of manuscripts is 1 September (for the April issue) and 1 March (for the October issue).**

**Format and Preparation.** Authors are strongly encouraged to submit manuscripts electronically to the editor at the email address below, and in the format specified below. On the upper left of the title page give name, address, telephone and fax numbers, and email address of the author to whom all correspondence is to be sent. The paper should have a concise and informative title, followed by the names and addresses of all authors. The sequence of material should be: title, author(s), abstract, text, acknowledgments, literature cited, appendix, figure legends, figure copies (each numbered and identified), tables (each numbered and with heading). Each of the following should start a new page: (1) title page, (2) abstract, (3) text, (4) literature cited, (5) figure legends, (6) footnotes.

Upon **final acceptance** of a manuscript, the author should provide the editor with an emailed IBM formatted electronic version. CD-ROMs or 3.5 inch floppy disks are acceptable. Because symbols and tables are not always correctly translated it is best to also send a printed copy of the manuscript. Preferred word processing programs are Microsoft Word and WordPerfect. If possible, all words that must be italicized should be done so, not underscored. Tables may be formatted in a spread sheet program such as MS Works or MS Excel. Text should be double-spaced typing, with 25 mm left and right margins. Tables should be put in a separate file. CDs and Diskettes should be accompanied by the name of the software program used (e.g., WordPerfect, Microsoft Word). Authors should keep backup copies of all material sent to the Editor. The Society cannot be responsible for diskettes or text mislaid or destroyed in transit or during editing.

Illustrations should be planned for reduction to the dimension of the printed page (14 × 20.5 cm, column width 6.7 mm) and allow room for legends at the top and bottom. Do not make plates larger than 14 × 18 in. (35.5 × 46 cm). Individual figures should be mounted on a suitable drawing board or similar heavy stock. Photographs should be trimmed, grouped together and abutted when mounted. Figure numbers should be on the plate. Include title, author(s) and address(es), and illustration numbers on back of each plate. Original figures need not be sent until requested by the editor, usually after the manuscript has been accepted. Reference to figures/tables in the text should be in the style "(Fig.1)" "(Table 1)". Measurements should be in the metric system.

Electronic plates may be submitted on disc, via email or uploaded to an ftp site (instructions will be given). They must be fully composited, labeled, and sized to fit the proportions of the journal page. Line art should be scanned at 1200 dpi (minimum input resolution is 600 dpi). Color or grayscale (halftone) images should have a dpi of 300-350. Color files should be in CMYK and not RGB. Graphics should be submitted as TIFF, Adobe Illustrator or EPS files. No PowerPoint or Word/WordPerfect files with images embedded in them are acceptable.

All papers must conform to the *International Code of Zoological Nomenclature*. The first mention of a plant or animal name should include the full scientific name including the authority. Genus names should not be abbreviated at the beginning of a sentence. In taxonomic papers type specimens must be clearly designated, type depositories must be clearly indicated, and new taxa must be clearly differentiated from existing taxa by means of keys or differential diagnoses. Authors are required to deposit all type material in

Recognized institutions (not private collections). Voucher specimens should be designated for specimens used in behavioral or autecological studies, and they should be deposited similarly. DNA sequences must be deposited in GenBank/EMBL/DNA Databank of Japan.

Acceptance of taxonomic papers will not require use of cladistic methods; however, authors using them will be expected to specify the phylogenetic program used, including discussion of program options used. A data matrix should be provided for morphological characters. Cladograms must be hung with characters and these should include descriptors (not numbers alone) when feasible. The number of parsimonious cladograms generated should be stated and reasons given for the one adopted. Lengths and consistency indices should be provided. Adequate discussions should be given for characters, plesiomorphic conditions, and distributions of characters among outgroups when problematical.

References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For multiple authors, use the word "and," not the symbol "&" (Smith and Jones 1999). For papers in press, use "in press," not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely and in italics.

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